ANNALS

OF THE

SOUTH AFRICAN MUSEUM

VOLUME XLII

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PRINTED FOR THE

TRUSTEES OF THE SOUTH AFRICAN MUSEUM

AND FOR THE

GEOLOGICAL SURVEY OF SOUTH AFRICA

1953 — 1956

BY THE NATIONAL COMMERCIAL PRINTERS LIMITED,

JAN VAN RIEBEECK STREET, ELSIES RIVER.

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LIST OF CONTRIBUTORS.

NEW GENERIC NAMES PROPOSED IN THIS VOLUME.

DATE OF ISSUE OF THE PARTS.

Part 1, April, 1953.
Part 2, January, 1954.
Part 3, January, 1955.
Part 4, March, 1956.

LIST OF PLATES.

LIST OF GENERA.

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SOUTH AFRICAN MUSEUM

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Descriptions of the Palaeontological Material collected by the South African Museum and the Geological Survey of South Africa.

PART I, *containing:—*

ISSUED APRIL 1953 *PRICE* 12*s*. 6*d*.

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BY THE RUSTICA PRESS LIMITED, COURT ROAD, WYNBERG, CAPE

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1. *A Note on some Rhynchosaurian Remains from Tanganyika Territory.* By Lieuwe D. Boonstra, D.Sc.

(With 2 text-figures.)

From Mr. G. M. Stockley I have received three tins containing fossil remains from near Msamara, in the Tunduru district of the Southern Province of Tanganyika Territory, for determination. This material (S7662) consists of weathered fragments of skull, limb-bones and vertebrae. The largest skull fragment consists of part of the left upper jaw. The limb-bones include a proximal third of a right femur, a weathered distal end of a femur, a bit of humerus, scapula and tibia. The vertebral material consists of the weathered centra of dorsal and caudal vertebrae showing few distinctive features.

Skull (fig. 1)

This weathered and rolled fragment consists of part of the left jugal, maxilla and palatine. On the lateral surface two nutritive foramina pierce the maxilla. The dentigerous border of the maxilla is convex antero-posteriorly. The ventral surface of the maxilla is studded with a large number of worn peg-like teeth varying in diameter from 2 to 4 mm. These teeth are somewhat indefinitely arranged, but there does appear to be some indication of an alignment in four rows. The teeth on the inner or lingual margin of the maxilla are aligned in a fairly definite row. On the outer or labial margin and anteriorly the teeth are larger than those situated medio-posteriorly. The width of the dentigerous surface is wider posteriorly than anteriorly. Medial to the maxillary teeth there lies a groove filled with matrix, and the maxillo-palatine suture would lie along this groove. Lingual to this groove there lies a row of teeth on the labial border of the palatine, with at least three more indefinite rows of teeth lingually. As is the case with the maxilla the width of the dentigerous surface is posteriorly wider than anteriorly. As preserved, the length of the maxillary dentigerous surface is 100 mm., the width anteriorly 7 mm. and posteriorly 20 mm.

The nature of the dentigerous plate of the maxillo-palatine indicates that we have here a fragment of a Rhynchosaurian skull showing particular affinities

to *Scaphonyx australis* described by Von Huene from South America, *Hyperodapedon gordoni* described by Huxley from Scotland, and *Hyperodapedon huxleyi* described by Lydekker from India. The length of the dentigerous surface in this specimen from Tanganyika is, as preserved, greater than in these three known forms.

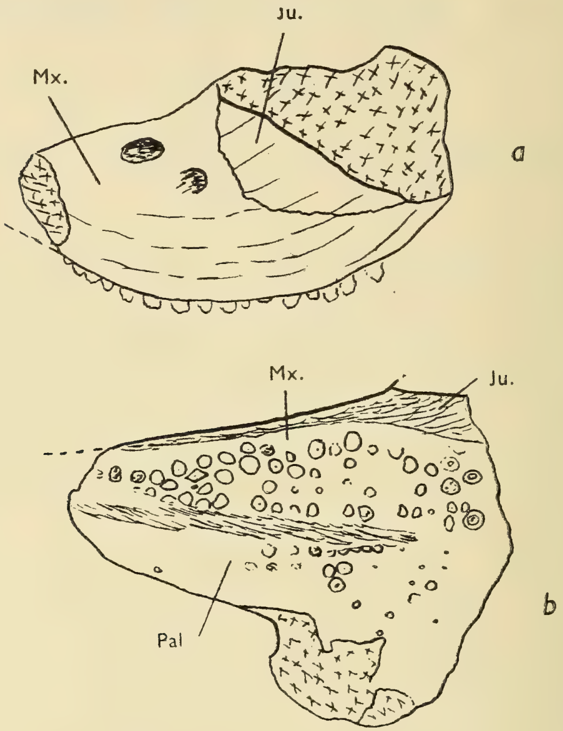


FIG. 1.—Maxillo-palatine complex of *Scaphonyx stockleyi*. *a*, lateral view ($\times \frac{1}{2}$). *b*, ventral view ($\times \frac{1}{2}$). S.A.M. 11704.

In *H. gordoni* the teeth are placed in rows much more definitely than in the Tanganyika specimen; in the former there are two rows on the maxilla whereas in the latter there are possibly four rows; and the width of the dentigerous surface of the maxilla is also smaller in *H. gordoni*.

In *H. huxleyi* the teeth are also in much more definite rows, and the number of rows on the maxilla exceed those on the palatine. In the Indian beast the crowns form triangular pyramids whereas in the Tanganyika beast the crowns are bluntly conical.

In *Scaphonyx australis* the teeth are of very similar shape and have very nearly the same arrangement. But, whereas the anterior maxillary teeth are larger than the posterior ones in the Tanganyika specimen, the reverse is the case in the South American specimen.

From the available evidence, admittedly scanty, it would thus appear that we have here a type distinct from all the hitherto known Rhynchosaurians, but apparently approaching fairly closely the skull fragment described by Von Huene from South America and by him referred to as *Scaphonyx australis*. I propose that the Tanganyika beast be included in Smith Woodward's genus *Scaphonyx*, but to be distinguished from the hitherto known species and to be known under the name *Scaphonyx stockleyi* n.sp.

Type.—Skull fragment in the South African Museum, S.A.M. 11704.

FEMUR (fig. 2)

The proximal third of a weathered right femur is preserved. The post-axial corner with the external trochanter is missing. Noteworthy features of this fragment are: the caput femoris is bent sharply dorsally; the internal tro-

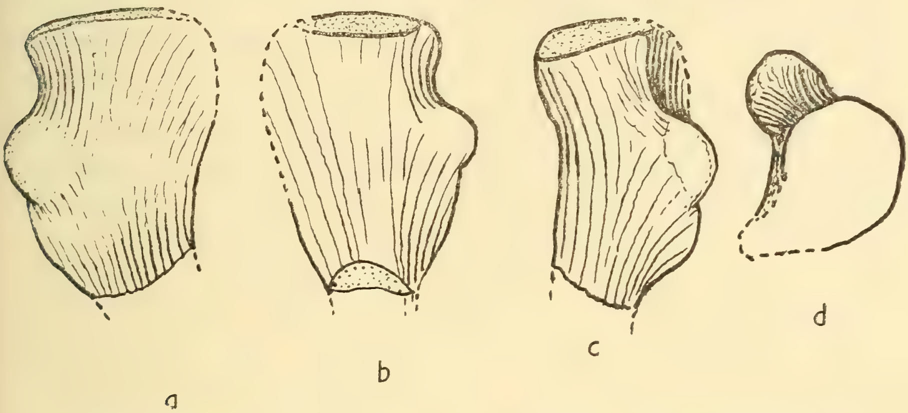


FIG. 2.—Proximal end of femur of *Scaphonyx africanus*. *a*, ventral view ($\times \frac{1}{2}$). *b*, dorsal view ($\times \frac{1}{2}$). *c*, pre-axial view ($\times \frac{1}{2}$). *d*, articular surface ($\times \frac{1}{2}$). S.A.M. 11705.

chanter forms a prominent bulbous structure and is abruptly demarcated from the caput, and is situated some distance distally from the proximal articulatory surface; the inter-trochanteric fossa is comparatively shallow, but, because of the curvature of the bone and the presence of a low ridge, is clearly separated from the more distal ventral surface of the bone; the proximal articulatory surface is wide dorso-ventrally; the external trochanter was probably not strongly developed and the ilio-femoralis flange not extensive.

This femur is about half the size of that (S344) described by Haughton under the name *Stenaulorhynchus stockleyi* but is obviously of a related type. Apart from the difference in size it differs in the shape of the caput; the internal trochanter is situated further distally; is more bulbous and is abruptly separated from the caput without a connecting neck. This femur, although also only half the size, shows closer affinities to that of *Scaphonyx fischeri* and *Scaphonyx australis* as described and figured by Von Huene. But here also the nature of the internal trochanter is strikingly different, and the femur cannot be considered as being that of either of these two South American species.

If Von Huene is correct in assigning his skull fragment and femoral fragment to the same species (*Scaphonyx australis*), we have a dentigerous plate of 80 mm. associated with a femur proximally 80 mm. wide. In the Tanganyika material we have a dentigerous plate of at least 100 mm., and we would thus expect that the associated femur would have a width proximally of about 100 mm. Actually the femur under consideration cannot proximally be of a greater width than 50 mm. The femur can thus only be of a younger beast or of a smaller species. The ossification of the femoral fragment does not appear to be that of an immature half-grown animal, and is thus in all probability that of a species of half the size of *Scaphonyx australis*. For this species I propose the name *Scaphonyx africanus*.

Type.—Proximal third of a right femur, S.A.M. 11705.

The discovery by Mr. Stockley of these definite Rhynchosaurian remains in Tanganyika, together with the Rhynchosaurian limb-bones of *Stenaulorynchus stockleyi* previously described by Haughton from Njalila, will enable the stratigraphists to attempt a closer correlation of these beds with those that have yielded the species of *Hyperodapedon*, *Scaphonyx*, and the other closely related genera. The discovery of better-preserved material may make it necessary to remove these species from the genus *Scaphonyx* to a new genus. Until such time I do not think it necessary to create a new genus for these African forms.

2. *A Report on a collection of Fossil Reptilian Bones from Tanganyika Territory.* By Lieuwe D. Boonstra, D.Sc.

(With 7 text-figures)

Introduction

Recently I received from Mr. G. M. Stockley eight cases of fossil reptilian bones collected from the Ruhuhu Coalfield region. This collection was obtained from three distinct localities. Those labelled S346 come from the Matomondo area, S559 from the Ngaka-Kingori Hill area, and S340 from the Njalila-Mkongeleko area. The geological horizon of the first two localities is given as the Lower 'Bone Bed' of the Songea Series, and the third as the Upper 'Bone Bed' of the same series.

Stockley states that the bones 'were picked up from the surface and thus are much weathered'. It is clear that all the fragments collected from a locality were given the same number, and each number undoubtedly includes fragments derived from a number of different skeletons. I have no means, other than the state of preservation, of determining the degree of association of the various fragments. For the greater part the fragments thus have to be considered individually. No evidence is given by the collector that the fragments bearing the same number were obtained or derived from the same horizon within the bed. On the contrary, it is evident on morphological grounds that from the Upper 'Bone Bed' there are at least four groups of specimens and that these were derived from four different levels within the bed. It should be stressed that in future collecting attention should be paid to the relative levels within the bed from which each specimen is collected.

A. Material from the Lower 'Bone Bed'

1. *Anomodont Skull Fragments*

Under the label S346 there are a small number of weathered pieces which include fragments identifiable as parts of a fairly large anomodont skull with a narrow parietal crest. This feature apparently excludes reference to the *Aulacephalodon* group of genera, and these fragments must thus represent a large species of the genus *Dicynodon*.

Under the label S559 there are a large number of weathered pieces—cranial as well as post-cranial. Of the recognizable skull fragments the following identifications have been possible, mainly on pieces of the intertemporal region bearing the pineal foramen and the structures immediately surrounding it.

(*a*) In one piece of the intertemporal region of a fairly large dicynodont there is a medium-sized oval foramen situated at the posterior end of a depression formed by the preparietal. The parietal crest is of medium width and height. The distinguishing feature in this fragment is the nature of the preparietal.

From the anterior border of the foramen the sides of the preparietal diverge in anterior direction. The preparietal thus meets the frontal in a long transverse suture. The whole of the bone lies in a depression. Direct comparison proved the identity of this specimen with a form from the Luangwa Valley of Northern Rhodesia which I described under the name *Dicynodon roberti*. This specimen now bears the South African Museum Cat. No. 11706.

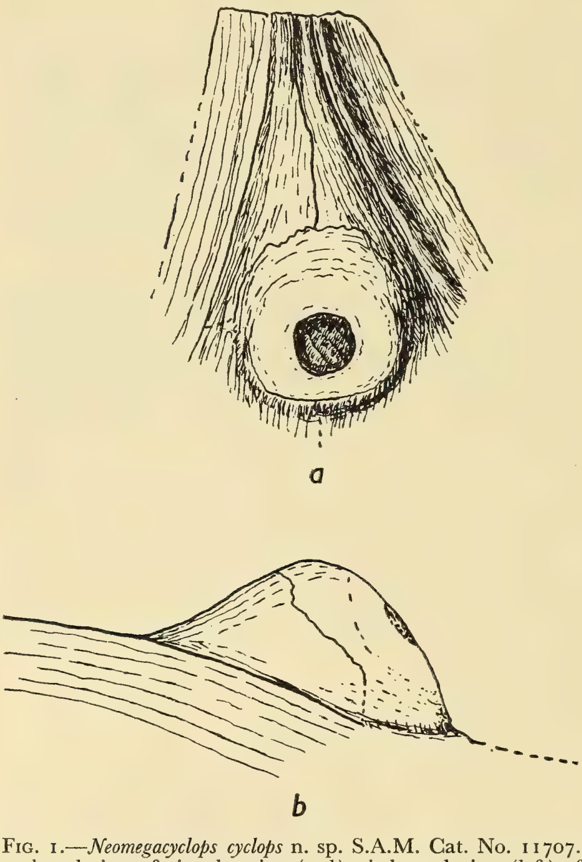


Fig. 1.—*Neomegacyclops cyclops* n. sp. S.A.M. Cat. No. 11707. *a*, dorsal view of pineal region (× ½). *b*, lateral view (left) of pineal boss (× ½).

(*b*) In another fragment (fig. 1) the pineal foramen pierces a large oval boss which is almost entirely formed by the preparietal. The posterior third of the boss is formed by the parietal, but this bone only stretches two-thirds up the posterior surface of the boss and is thus excluded from the border of the pineal foramen. The preparietal completely surrounds the foramen, which is of medium size and nearly circular. The foramen is directed anteriorly, and the plane in which it lies makes an angle of 45° with the plane of the dorsal surface of the skull. Posteriorly, the surface of the boss, here formed mainly by the parietal, slopes gently backwards. The parietal, which has only a small exposure, is then covered by the two post-orbitals which meet on the median line. Anteriorly, the boss is abruptly marked off from the surface of the frontals by a semicircular groove. A near approach to this condition of the pineal region, in the more fully known Karoo species, is shown by some of the species of the genus *Platycyclops*, where the foramen is also completely surrounded by the preparietal raised in the form of a boss. A nearer approach still is shown in the species of the genus *Megacyclops*, where the parietal participates in and forms the posterior part of the boss. In the present specimen the shape of the boss differs remarkably

from that of *M. whaitsi* of the South African Karoo and of *M. rugosus* described by Haughton from Tanganyika, but agrees in other features, particularly in being so definitely anteriorly directed and in the manner in which the parietal participates in its formation. It differs from *M. usiliensis* of Von Huene in the slope of the boss and in the fact that the parietal is excluded from the border of the foramen. It is thus evident that we have here a new species of *Megacyclops** and this fragment can be designated as the type specimen of *Neomegacyclops cyclops* n. sp. This specimen now bears the South African Museum Cat. No. 11707.

(*c*) In a third fragment where the intertemporal region is preserved, the nature of the pineal region is strongly reminiscent of that known in the genus *Rachiocephalus* of the *Endothiodon* zone of the South African Karoo and may be provisionally referred to that genus. This specimen now bears the South African Museum Cat. No. 11708.

(*d*) Another identifiable fragment is of the central part of a massive occiput. The basisphenoidal tubera are exceptionally massive and are, furthermore, peculiar in that they lie practically horizontally instead of approaching the vertical, so that the *foramen ovale* is directed nearly completely posteriorly, whereas the more usual direction is nearly completely ventrally. This condition is not known to exist in the genera *Megacyclops* and *Rachiocephalus*. This fragment is thus not derived from either of the large skulls that yielded the pineal regions mentioned above. In none of the larger Anomodonts examined by me nor in the published descriptions have I seen basisphenoidal tubera of a similar nature. This fragment thus indicates the existence in Tanganyika of a new type of the larger Anomodonts, of which one hopes that a more complete skull may soon be found and be designated as the type of this new species. This specimen now bears the South African Museum Cat. No. 11709.

2. *Anomodont Limb-bones*

Included in the collection are a number of weathered distal and proximal ends of some large humeri, femora and ulnae. The former two are of about the same size and nature as the humerus and femur described by Haughton and referred to as *Eocyclops*? and *Megacyclops* respectively. In addition to these there are some proximal and distal ends of humeri and femora of Anomodonts of smaller size which could be associated with a skull of the size of a form like *Dicynodon huenei*—a species peculiar to Tanganyika. These specimens now bear the South African Museum Cat. Nos. 11710 and 11742.

3. *Pareiasaurian Vertebrae*

Two medium-sized vertebrae are preserved in a weathered condition. These are typically Pareiasaurian, and are smaller than those of the larger genera which predominate in the *Tapinocephalus* zone of the Union. They are also

* I find that the name *Megacyclops* which Broom (1931) proposed for this anomodont genus is preoccupied for a crustacean (Kiefer, 1927). I propose that this anomodont genus be known under the new name *Neomegacyclops* nom. nov.

smaller than, and do not show the peculiarly narrow elongated dorsal spine so characteristic of, the vertebrae described by Haughton from locality B19, west of Kingori. These vertebrae prove the presence in Tanganyika of Pareiasaurs probably closely related to the medium-sized types of the South African Karoo. These now bear the South African Museum Cat. No. 11743.

4. *Therapsid Cranial Material*

Among the mass of weathered fragments from the Ngaka-Kingori Hill area there are two incomplete snouts much weathered, and one fairly complete but

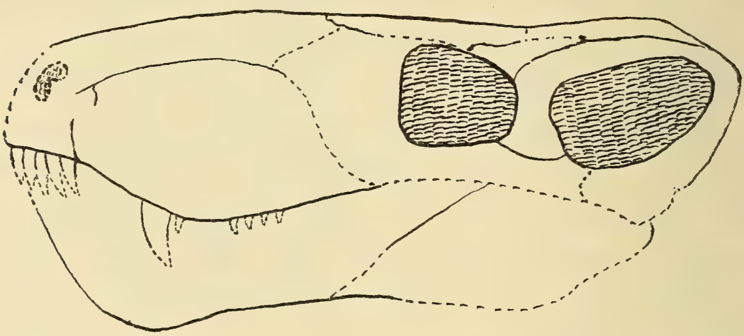


FIG. 2.—*Tangagorgon tenuirostris* n. g. et n. sp. S.A.M. Cat. No. 11744. Lateral view of skull (× ½).

somewhat distorted and weathered skull. The more complete skull is of a Gorgonopsian and the two snouts appear to be Therocephalian.

(*a*) The more complete specimen (figs. 2 and 3) has the outer surface considerably eroded, so that it is difficult to determine the sutures. The skull is of medium size. The chief measurements are:

Maximum length	190	mm.
Basioccipital—Premaxilla	184	,,
Premaxilla—Pineal foramen	145	,,
Premaxilla—Orbit	104	,,
Width across squamosals	95	,,
Interorbital width	49	,,
Intertemporal width	53	,,
Width across canines	40	,,
Height from Mx. edge—median suture	50	,,
Height of mentum	?40	,,
Length of molar series: Left (4 teeth)	17	,,
Right (3 teeth)	17	,,
Length of incisor series	25	,,

Dental formula: Right, i5, co+1, m3.
Left, i5, c1+1, m4.

The snout is long, high and narrow. Anterior to the orbits the cross-section is squarish. The orbits are situated in the posterior half of the skull and are laterally directed. The temporal openings are of medium size, oval, and directed as much dorsally as laterally. The pineal foramen is small and posteriorly situated. The frontals apparently form only a small part of the orbital border. The snout is higher than wide. The maxilla is deep. The interparietal is only slightly inclined downwards from the general dorsal surface and is more a bone of the dorsal surface than of the occiput. From the posterior edge of the interparietal the occiput descends practically vertically. The nature of the rest of the occiput is obscured by the presence of the proatlantal arches, atlas and axis. The teeth are poorly preserved. On the left there are preserved five medium-sized incisors, a fairly weak canine with the tip of a replacing? canine just emerging, and the roots of four small molars. On the right side the last of the five incisors is small (a replacing tooth?), the canine has been lost and a replacing? one is emerging; the crowns of three small molars are preserved, number 3 having fallen out.

The characters enumerated above do not occur together in any known Gorgonopsian, and I therefore designate this specimen as the type of a new genus and species—*Tangagorgon tenuirostris*. This type specimen now bears the South African Museum Cat. No. 11744.

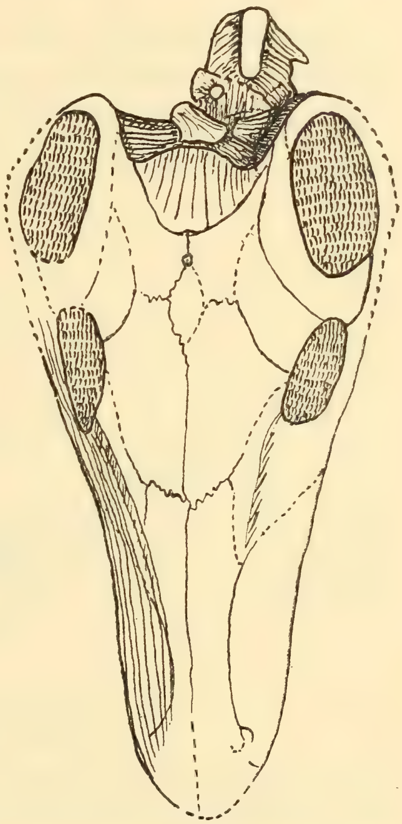


Fig. 3.—*Tangagorgon tenuirostris* n. g. et n. sp. S.A.M. Cat. No. 11744. Dorsal view of skull with proatlas, atlas and axis. ($\times \frac{1}{2}$)

(*b*) The smaller snout fragment is nearly completely stripped of bone but shows the roots of five strong and large incisors. This specimen, which is probably Therocephalian, now bears the South African Museum Cat. No. 11745.

(*c*) The larger snout fragment (fig. 4) represents the anterior half of a medium-sized skull. The tip of the snout is weathered away and no upper incisors are preserved. The lower edge of the dentary is also weathered away. A moderately sized canine is represented by a root, and four irregularly spaced and directed molars are present. The molars are implanted on a flange of bone lying in a plane medial to the general lateral maxillary surface. The lacrymal is of small antero-posterior extent and its intra-orbital surface is pierced by two

foramina. The accompanying sketch gives the general shape and proportions. The affinities of this Therocephalian are uncertain, but the nature of the lacrymal indicates that it is not a very primitive form, and that its affinities would lie with the Therocephalian forms younger than those from the *Tapinocephalus* zone. This specimen now bears the South African Museum Cat. No. 11746.

B. Material from the Upper 'Bone Bed'

Under the field number S340 there were six cases of weathered fragments. The majority of these, mostly small pieces, are so worn as to be indeterminable. In the workshop few contacts were found and only a small number could be fitted together. The determinable pieces consist of cranial fragments, a large number of vertebrae, parts of the pelvic and shoulder girdles, three complete

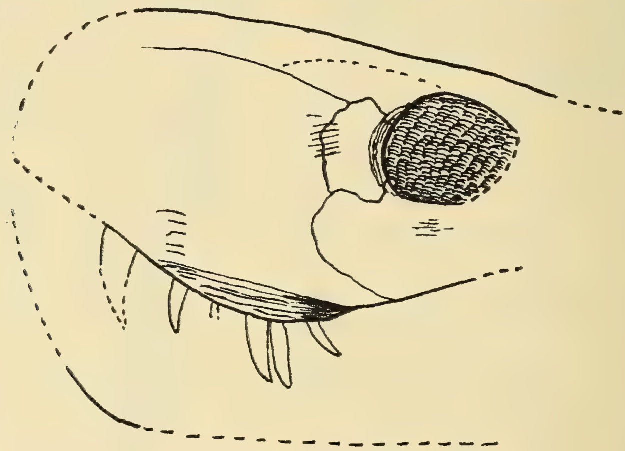


Fig. 4.—Therocephalian sp. S.A.M. Cat. No. 11746. Lateral view of incomplete and weathered snout. (× ½)

limb-bones and a large number of ends of various limb-bones. The following reptile groups are represented: Pareiasaurians, Anomodonts, Rhynchosaurians, Pseudosuchians, Cynodonts, and a Theropodous Dinosaur.

1. *Pareiasaurians*

Of this group there is preserved a single weathered distal end of a small right humerus. It is much smaller than the specimen from Tanganyika figured by Haughton and described under the new specific name *Anthodon minusculus.* In Haughton's specimen the greatest width across the condyles is 87 mm., whereas in this specimen it is only 63 mm. In all other determinable features the two specimens agree very closely. It would thus appear that we have here a humeral end of a smaller species or more probably of a juvenile specimen of *Anthodon minusculus.*

In the material from Tanganyika described by Haughton some errors of labelling are mentioned by him. The type specimen bears the number S342

and a second specimen the number S350; the former number being given to specimens from a locality (Njalila) in the Upper 'Bone Bed' and the latter number to specimens from a locality (below and west of Kingori) in the Lower 'Bone Bed'. Haughton assumed the number S342 to be an error in the labelling. Now, the present specimen bears the number S340, which refers to a locality (Njalila-Mkongeleko) in the Upper 'Bone Bed'. The weight of evidence in regard to the labelling is thus that all these specimens are derived from the Upper 'Bone Bed'. Palaeontologically, however, the Lower 'Bone Bed' is the horizon indicated, unless we consider it probable that this species survived practically unchanged into the Upper 'Bone Bed'. Until this uncertainty is removed these specimens must be cited with caution in drawing stratigraphical or faunistic conclusions.

2. *Anomodonts*

Fragments of skulls, lower jaws and various limb-bones prove the presence in these beds of species of medium sized to large Anomodonts.

(*a*) A well-preserved right humerus of medium size (fig. 5) can, despite the paucity of our knowledge of the post-cranial skeleton of the numerous species of Anomodonts, be referred to the genus *Lystrosaurus*. The distal condyles are undeveloped, the antero-ventral line is only weakly indicated, the lateral median line undeveloped, and no definite scar for the medial humeral head of the triceps is present. These characters exclude the terrestrial genera of the Anomodonts, and agree with the condition manifested in the species of the genus *Lystrosaurus*. In the absence of a skull no specific determination is possible, and it is advisable, until further data are available, to refer to this specimen as *Lystrosaurus* sp. The chief measurements are:

Greatest length	140 mm.
Greatest proximal width	77 „
Greatest distal width	91 „
Shaft	33 by 35 mm.

This specimen now bears the South African Museum Cat. No. 11748.

(*b*) Under the number S340 are included about a dozen ends of limb-bones. Among these are seven distal and three proximal ends of humeri, three distal and two proximal ends of femora which, with slight individual differences, agree well with the corresponding bones of *Kannemeyeria*. The widths across the distal ends of the humeri are: 180, 160, 158, 154, 148, 139 and 125? mm. These humeral ends are manifestly different from the humerus figured by Haughton under the name *Eocyclops*(?) sp. These specimens now bear the South African Museum Cat. No. 11749. Some fragments of the pelvic and pectoral girdle may also very well belong to this genus. In addition to these limb-bones there are also preserved the ends of much smaller Anomodont humeri and femora. So that, contrary to our experience in the South African Karoo, small Anomodonts survived comparatively late in Tanganyika. These bones now bear the South African Museum Cat. No. 11750.

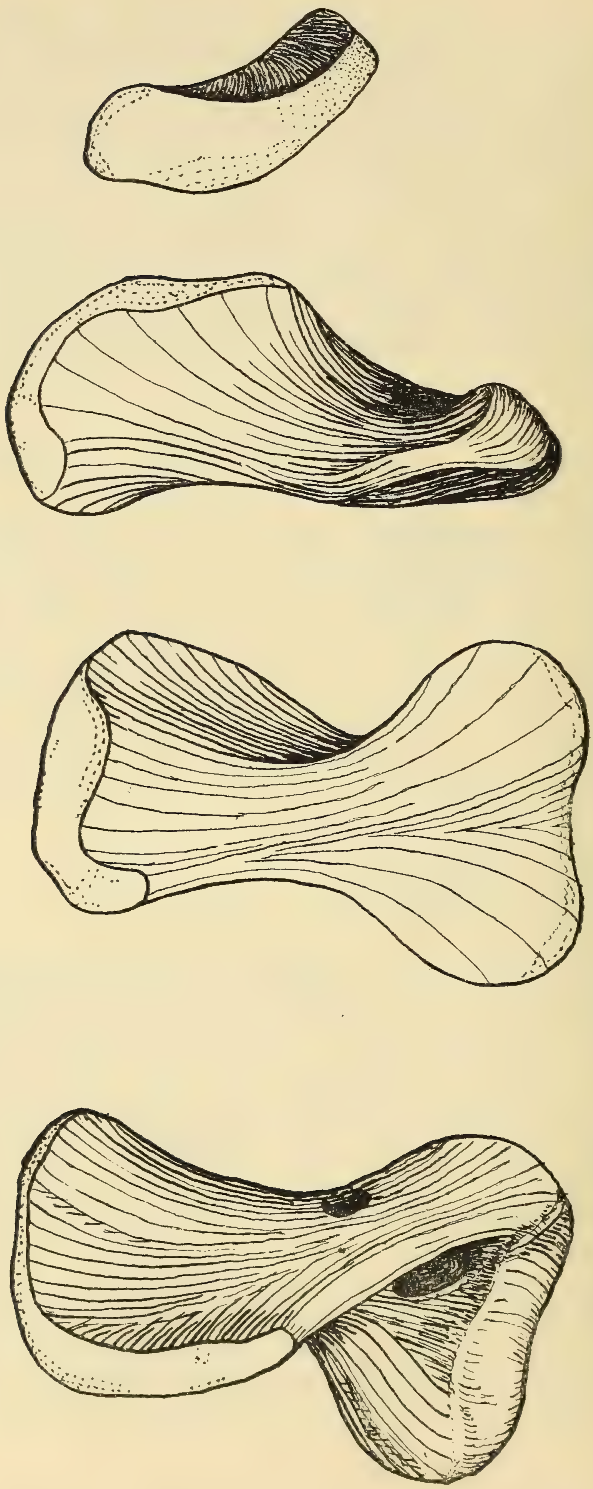


Fig. 5.—*Lystrosaurus* sp. S.A.M. Cat. No. 11748. Right Humerus in ventral, dorsal, anterior and proximal views (× ½).

(*c*) The Anomodont cranial material includes parts of the temporal arches, a quadrate, and some pieces of occiput. One occiput, with its tripartite condyle and its characteristically shaped and ventrally directed basisphenoidal tubera nearly surrounding the foramen ovale, is strongly reminiscent of the same structures in the skull of *Kannemeyeria* and may with confidence be referred to that genus. Some pieces of maxilla with the canine roots preserved may also be included in this determination. These fragments now bear the South African Museum Cat. No. 11751.

(*d*) Three other occipital fragments are more massive. Here the condyle is rounded with no grooves tripartitioning it. The basioccipital tubera, though massive, do not descend so far ventrally and are situated some distance apart. A very similar condition is shown by a number of the larger *Aulacephalodon*-like forms, but as in the large number of described forms this area is neither figured nor described, closer comparison is not possible, and for more specific determinations it is necessary that we have better descriptions of known forms or better-preserved skulls from this area. These specimens now bear the South African Museum Cat. No. 11752.

3. *Cynodonts*

One very badly eroded fragment consists of the anterior two-thirds of a fairly small Cynodont skull. The outer surface is so badly weathered that the structure is indeterminable, and on the palatal surface little more than the teeth sockets are preserved. These indicate that we have here a specimen of the genus *Trirachodon*. This specimen now bears the South African Museum Cat. No. 11755.

4. *Rhynchosaurians*

The collection includes the following bones, or parts of bones, determinable as Rhynchosaurian: a complete humerus, two proximal and seven distal ends of humeri, six proximal and four distal femoral ends, parts of the pelvic and pectoral girdles, a large number of disarticulated vertebrae, a jaw fragment and two incomplete occiputs.

(*a*) *The Humerus* (fig. 6).—Direct comparison of these humeral elements to the type humeral end of *Stenaulorhynchus stockleyi* proves them to be specifically identical. In size and in the proportions there are considerable differences in the hitherto described material and that at present under consideration, as will be apparent from the following table:

	Type	*Para-type*	*Huene's Spec.*	*Spec. a*	*Spec. b*	*Spec. c*	*Specs. d*	*e*	*f*
Max. length	?	?	145	166	?	?	?	?	?
Max. width across prox. end	101	77	92	110	120	?	?	?	?
Shaft	41×30	21×17	25×20	32×24	?	?	?	?	?
Proc. lat.—prox. end	83	57	60?	81	94	?	?	?	?
Proc. med.—prox. end	85	63	88?	101	110	?	?	?	?
Thickness at med. corner	37	26	33	31	40	?	?	?	?
Max. width across dist. end	?	?	80	100	?	93	80	78	97

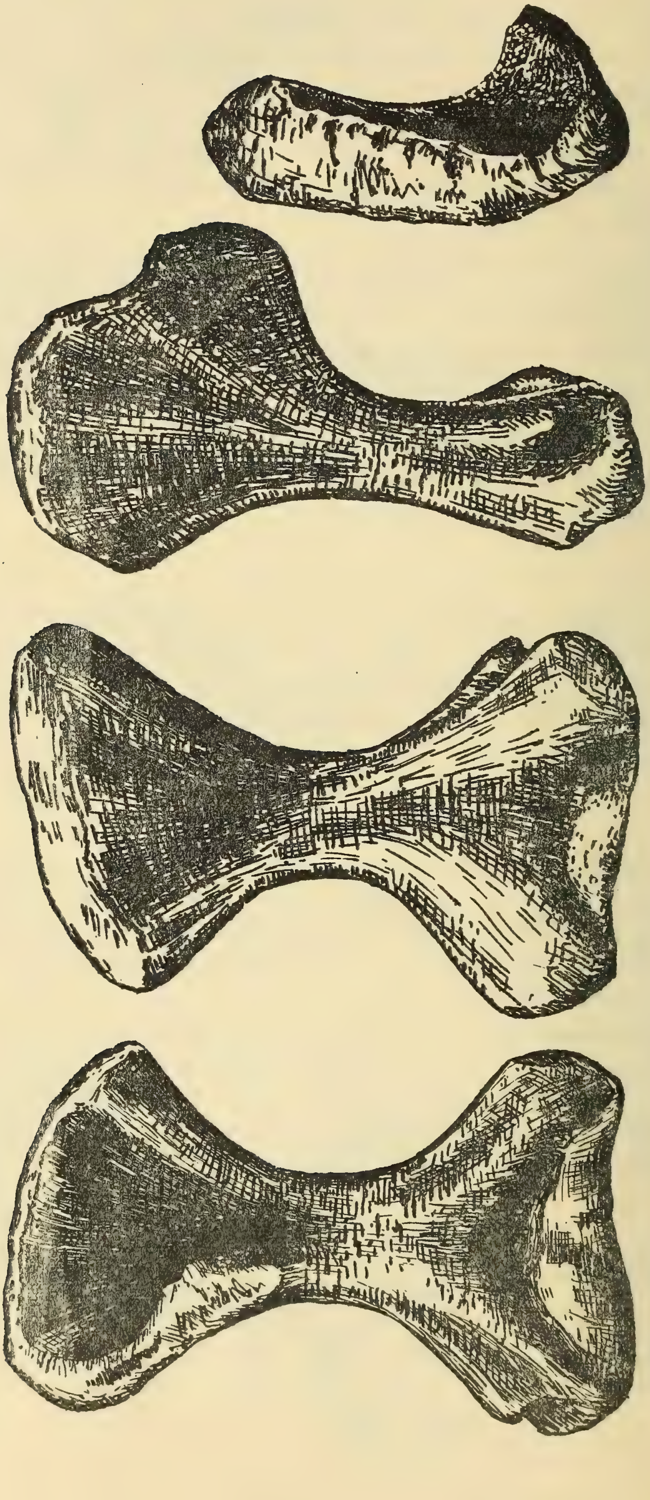


Fig. 6.—*Stenaulorynchus stockleyi*. S.A.M. Cat. No. 11753. Right Humerus in ventral, dorsal, anterior and proximal views (× ½). Drawing by Dr. A. J. Hesse.

In the light of our present limited knowledge it is advisable to consider these differences of size and proportions as age and/or sex variations and not as denoting any specific distinctness.

(*b*) *The Femur.*—In the collection there are six proximal and four distal ends of femora. Direct comparison with the type material proves these bones to be specifically identical to Haughton's *Stenaulorhynchus stockleyi.* As in the type material there is considerable variation in the various dimensions:

	a	*b*	*c*	*d*	*e*	*f*
Max. width over trochanter .	93	73	72	71	65	64
Max. thickness of prox. end .	58	?	44	53	48	52
Trochanter—prox. end . . .	37	?	33	15	22	31

There is, moreover, considerable variation in point of size, shape and position of the trochanter:

In *a* the slightly bulbous trochanter is connected with the proximal surface by a somewhat constricted neck.

In *b* the trochanter is less bulbous and the neck less constricted.

In *c* the trochanter is hardly thickened, and instead of a neck a sharp ridge connects it to the proximal surface.

In *d* the trochanter lies nearly in the same plane as the proximal surface, and in proximal view appears as a tongue-like extension of the proximal surface, without any neck.

In *e* the bulbous trochanter connects with a short neck to the side of the proximal end to form a distinct step.

In *f* a thickened ridge attaches the trochanter to the proximal end.

In the specimen recently described by me under the name *Scaphonyx africanus* the bulbous trochanter is separated from the proximal surface by a much greater step than in *e*. The amount of variation shown by the above specimens impels one to reconsider the position of *Scaphonyx africanus*. This must now be considered as an extreme variant of a femur of *Stenaulorhynchus stockleyi*, and the name given by me becomes a synonym of *Stenaulorhynchus stockleyi* Haughton.

The distal femoral ends of our material agree very well with that of the type material and the shaft of one specimen with that figured by Von Huene.

(*c*) *The Girdles and Vertebrae.*—The material here preserved agrees in all essentials with the corresponding bones figured by Von Huene in his paper on *Stenaulorhynchus*.

(*d*) *The Occiput.*—Included in the material there are two imperfect and weathered occipital fragments that appear to be identical to the occiput described by Von Huene and figured in fig. 4 in his paper on *Stenaulorhynchus* and in fig. 6 in his 'Die Verwantschaftsgeschichte der Rhynchosauriden des Südamerikanischen Gondwanalandes'. A very eroded fragment in a different type of matrix shows a part of the maxilla and dentary which also appears to be Rhynchosaurian. All these Rhynchosaurian bones now bear the South African Museum Cat. No. 11753.

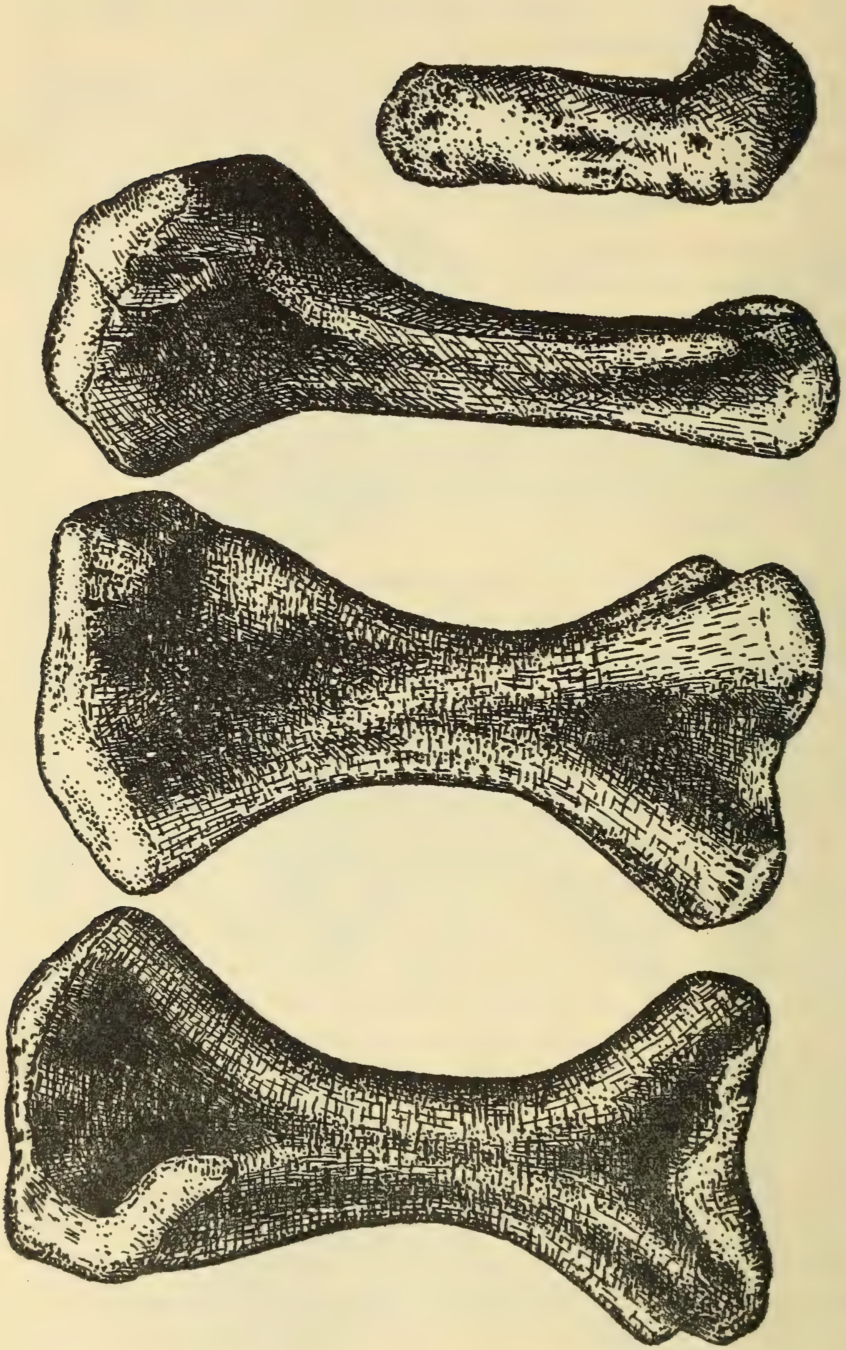


FIG. 7.—*Stagonosuchus tanganyikaensis* n. sp. S.A.M. Cat. No. 11754. Right Humerus in ventral, dorsal, anterior and proximal views ($\times \frac{1}{2}$). Drawing by Dr. A. J. Hesse.

5. *Pseudosuchians* (fig. 7)

Also bearing the field number S340 is a well-preserved right humerus. This bone shows undoubted and close relationship to the corresponding bone in the material collected by Dr. Nowack in the Njalila area, and included in the type material described by Von Huene under the name *Stagonosuchus nyassicus*, and representing a new genus and species of Stagonolepid Pseudosuchians. Although closely resembling Von Huene's form, the following comparative table of measurements in mm. will show that some noteworthy differences in size and proportions exist:

	St. nyassicus	*St. tanganyikaensis*
Maximum length	320	200
Max. width across prox. end . .	180	112
Max. width across dist. end . . .	130	93
Max. width of shaft	50	38
Proc. lat.—prox. end	70	52
Ectepicondylar flange—dist. end .	30	23

These differences appear to be of a specific nature, and I propose that this new species be known under the name *Stagonosuchus tanganyikaensis*. The main points of difference between *nyassicus* and *tanganyikaensis* may be enumerated: in *nyassicus* the processus lateralis lies in the same plane as the median corner of the proximal surface, whereas in *tanganyikaensis* the medial corner is not deflected and thus not situated so far distally; in *tanganyikaensis* the bicipital fossa is deeper and circumscribed much more definitely; the angle between the planes in which the proximal and distal ends lie is less in *tanganyikaensis* than in *nyassicus*; proportionally the distal end is wider, the shaft has a greater maximum width and is relatively shorter, the processus lateralis extends further distally in *tanganyikaensis* than in *nyassicus*. This humerus now bears the South African Museum Cat. No. 11754.

6. *Dinosaurs*

Among the large number of Rhynchosaurian vertebral elements in this collection I found a fairly small caudal vertebra lacking the upper part of the neural spine, of a Theropodous Dinosaur. The chief measurements are:

Greatest length of centrum	40 mm.
Greatest height of centrum	34 ,,
Greatest width of centrum	28 ,,

I have compared this vertebra with the *Thecodontosaurus* caudal vertebrae in our Museum and find a fairly close agreement, especially with the anterior caudals of a specimen from the Red Beds of the Stormberg Series of the Union. This specimen now bears the South African Museum Cat. No. 11793.

Conclusions

From the above account it is thus evident that in this collection there are from the Lower 'Bone Bed' no forms showing any close relationship to the fauna of the *Tapinocephalus* zone. The Anomodonts, Pareiasaurs and Therapsids it

contains are all manifestly akin to species from the *Endothiodon* and *Cistecephalus* zones of the Karoo of the Union. The beds represented in the Matomondo and Ngaka-Kingori Hill areas are thus homotaxial to the upper two zones of the Lower Beaufort of the Union.

The assemblage from the Upper 'Bone Bed' of the Njalila-Mkongeleko area, containing as it does small to medium-sized Anomodonts, Anomodonts of the Aulacephalodon group, a Lystrosaur, a *Kannemeyeria*, a Cynodont, a Rhynchosaurian, a Pseudosuchian and a Theropodous Dinosaur, is related to the fauna known from the beds of the Karoo ranging from the top of the *Cistecephalus* zone of the Lower Beaufort right up to the Red Beds of the Stormberg. A more detailed recording of the relative levels in which the various fossils occur will enable the stratigrapher to subdivide the Upper 'Bone Bed' of this area into beds respectively homotaxial to the Middle and the Upper Beaufort, the Molteno and the Red Beds. It is probable that in this area some of the Anomodonts were actually derived from the top of the Lower Beaufort.

Acknowledgments

My thanks are due to Mr. G. M. Stockley and his collectors for the opportunity of examining this interesting collection, and to Dr. A. J. Hesse for two of the illustrations.

REFERENCES

Boonstra, L. D. 'A Report on some Karroo Reptiles from the Luangwa Valley, Northern Rhodesia', *Q.J.G.S.*, xciv. 1938.

Boonstra, L. D. 'A Note on Some Rhynchosaurian Remains from Tanganyika Territory', *Ann. S. Afr. Mus.*, xli, p. 1. 1952.

Broili, F., and Schröder, J. 'Beobachtungen an Wirbeltieren der Karrooformation, xxiv, and 'Über Theriodontier-Reste aus der Karrooformation Ostafrikas', *Sitzb. Bay. Akad. Wiss.* 1936.

Haughton, S. H. 'On Karroo Vertebrates from Nyasaland', *Trans. Geol. Soc. S. Afr.*, xxix. 1926.

Haughton, S. H. 'On a Collection of Karroo Vertebrates from Tanganyika Territory', *Q.J.G.S.*, lxxxviii. 1932.

Huene, F. von. 'Über Rhynchosaurier und andere Reptilien aus den Gondwana Ablagerungen Südamerikas', *Geol. Pal. Abh.*, 17/1/1929.

'Kurzer Überblick über die terrestrischen Wirbeltierfaunen der jungeren Gondwanazeit', *Centr. f. Min. usw.*, Abt. B, No. 6. 1933.

'*Stenaulorhynchus*, ein Rhynchisauride der Ostafrikanischen Obertrias', *Nova Acta Leopoldina*, vi, 36. 1938.

'Ein grosser Stagonolepide aus der jungeren Trias Ostafrikas', *N. Jahr. f. Min. usw.*, Bd. 80, Abt. B. 1938.

'Die Alterbeziehungen der südamerikanischen Gondwana Fauna', *Physis.*, xiv. 1939.

'Die Lebensweise der Rhynchosauriden', *Pal. Zeit.*, xxi, 3. 1939.

'Die Karroofauna im ostafrikanischen Ruhuhu Gebiet', *Zentrbl. f. Min. usw.*, Abt. B No. 2. 1939.

'Ein kleiner Pseudosuchier und ein Saurischier aus den ostafrikanischen Mandaschichten', *N. Jahr. f. Min. usw.*, Bd. 81, Abt. B. 1939.

'Die Verwantschaftsgeschichte der Rhynchosauriden des südamerikanischen Gondwanalandes', *Physis.*, xiv. 1939.

'Die Saurier der Karroo-, Gondwana- und verwandten Ablagerungen in faunistischer, biologischer und phylogenetischer Hinsicht', *N. Jahr. f. Min. usw.*, Bd. 83, Abt. B. 1940.

'Die Anomodontier des Ruhuhu-Gebietes in der Tübinger Sammlung', *Palaeontographica*, xciv. 1942.

'Pareiasaurierreste aus dem Ruhuhu-Gebiet', *Pal. Zeit.*, xxiii, 3/4. 1944.

Parrington, F. R. 'On the Tooth-Replacement in Theriodont Reptiles', *Phil. Trans. Roy. Soc.*, B, 226, 532. 1936.

'On the Cranial Anatomy of Cynodonts', *P.Z.S.*, cxvi, 2. 1946.

Young, C. C. 'The Triassic Vertebrate Remains of China', *Am. Mus. Nov.*, No. 1324. 1946.

3. *A suggested clarification of the Taxonomic Status of the South African Titanosuchians.*

By Lieuwe D. Boonstra, D.Sc.

(With Plates I–IX)

Introduction

Being engaged on a morphological study of the Deinocephalians the need has arisen to establish some order in the systematics of the group. In an assessment of the importance of the various morphological features the existence of a number of generic and specific names, not associated with at least some of the main morphological characters, is merely confusing and an encumbrance.

In the literature there are about half a dozen generic and a somewhat greater number of specific names that signify next to nothing. One is led to wonder why they were ever created at all. One realizes that due to the nature of the material dealt with in palaeontology, it is not always possible to describe only relatively well-preserved specimens. There is some justification, although one doubts the wisdom, if a newly discovered fragment establishes the existence of a group hitherto unknown to science (as, for instance, Owen's creation of *Titanosuchus ferox*), but there is no justification for subsequent authors to create additional names for specimens that do little more than prove that there are more individuals of the group besides the original individual. It is, of course, fully realized that the vertebrate palaeontologist generally deals with individuals and that his species mostly refer to single individuals and are hardly ever the norm of a good series.

In the Titanosuchians sixteen generic names have been created up to date. Of these only five (*Jonkeria*, *Dinosphageus*, *Anteosaurus*, *Dinophoneus*, and *Dinosuchus*) are based on reasonably fully preserved skulls, one (*Phoneosuchus*) on a good lower jaw, and the other ten (*Titanosuchus*, *Archaeosuchus*, *Dinartamus*, *Scapanodon*, *Lamiasaurus*, *Dinocynodon*, *Enobius*, *Scullya*, *Dinopolus*, and *Titanognathus*) are all based on either skull fragments or parts of dentaries.

In two former papers, in 1935 and 1936, I have shown that two of the above names must fall away—*Dinophoneus* and *Phoneosuchus* being both synonyms of *Jonkeria*. In the sequel a further reduction of generic names will be proposed.

At this stage I am only considering the cranial material on which, in any case, the authors have mainly created their new genera and species. I have critically examined most of the described specimens and for the rest have extracted the pertinent points from the descriptions of the authors concerned. In addition there is at the South African Museum a large collection, mainly collected by myself in recent years, of undescribed material which includes a dozen or so really good skulls. I now wish to present tentatively, for criticism by colleagues, a solution of the taxonomic maze formed by the plethora of names. With due

regard to the fetish of the law of priority I have attempted to include as many of the fragmentary specimens as is possible instead of simply regarding them as generically or specifically indeterminate.

Sex and Age in the Titanosuchians

In addition to the fragmentary nature of many of the types there are other difficulties in arriving at a reasonable classification. With the small number of individuals known we have little to indicate sex in the Titanosuchians. It must, however, be kept in mind that a smaller size, lighter build and a lesser degree of pachyostosis, particularly with regard to bosses, may indicate the female of the species.

Without a reasonably long series of specimens it is difficult to determine the effects of age in the Titanosuchian skull. In the Tapinocephalian, *Moschops*, Gregory found an increasing pachyostosis, especially of the postorbital bar, a character indicating increasing age. In some of the Titanosuchians, especially of the *Anteosaurus* group, there is a slight variation in the thickening of the postorbital bar, but whether this is due to age or sex is uncertain. In the *Jonkeria* group there are marked differences in size unaccompanied by other differences of generic value. Here size is not considered a character of generic value and at most may be regarded as specific, but in some cases may very well be a character of full maturity. Thus *Dinosphageus* is considered to be a large species of *Jonkeria*, but may very well prove to be a fully grown specimen of one of the previously described species of *Jonkeria*. The strength and size of the dentary, particularly of the mentum, have been used as a character of systematic value, but is it not probable that a moderately strong dentary with a sloping mentum may become massive with a fairly upright mentum with increasing age? This was one reason for regarding the name *Enobius* as unnecessary.

The Dentition

The dentition of the Deinocephalians presents some very interesting conditions. A detailed study of the modifications and their implications should be undertaken. Here I can only touch on some aspects. A study of the teeth is made very difficult because of the poor preservation in most specimens. In the majority of cases the crowns are not preserved and we are forced to study stumps and cross-sections at varying levels which are not directly comparable. The presence of a lingual crushing surface internal to a talon in many teeth very materially affects the nature of the cross-section at different levels. Where crowns are preserved the intractable nature of the matrix of the *Tapinocephalus* zone makes it difficult to free them from the matrix satisfactorily.

The Titanosuchians have a heterodont dentition with incisors, canine and postcanines. In some forms the incisors are fairly short with a labial talon and a lingual crushing surface, in others the incisors are long to very long with a talon long to very long and the lingual crushing surface is poorly developed or represented only by a cingulum, or wholly absent. The canines are strong to

very strong, simple, pointed teeth of a typical carnivorous nature with, in some cases, a possibly serrated posterior cutting edge. What little is known of the postcanines indicates a considerable variation in the nature of the crowns—some have flattened crowns with serrations, others short or longish conical teeth.

Now, is the heterodont Titanosuchian dentition to be morphologically derived from the homodont dentition of the Tapinocephalians? The Tapinocephalian teeth all have a talon, pointed or somewhat flattened, and a lingual crushing surface varying in strength, from which the different Titanosuchian types of teeth could be morphologically derived. The medium-sized incisors of a form like *Jonkeria*, with its short talon and definite lingual crushing surface, would then represent a more primitive stage than the long incisors of some of the Anteosaurians which are all talon with no crushing surface. The stages in this transition could then be used for taxonomic purposes. But, in *Dinartamus*, Broom found a mixture of these two types of incisors and the question arises whether this may not represent a difference in the consecutive sets of incisors. We do not know how many times the Titanosuchians replaced their incisors. Hitherto only two sets have been described. On this subject the external nature of the teeth gives little information and we have to rely on fortuitous weathering and fracturing or sectioning. The material at my disposal affords no evidence as to whether the Jonkerian type of incisor is the deciduous type and the Anteosaurian type typical of a later set of teeth. Until we have evidence supporting Broom's observations on *Dinartamus* I propose to consider the presence or absence of the lingual crushing surface in the incisors to be a specific character present in the consecutive sets of teeth, and not dependent on age.

Besides having these two types of incisors the Titanosuchians also possess a variable number of incisors—as described, from 0 to 5. In those specimens where the premaxilla is edentulous the condition can be interpreted in a number of ways: the incisors may have been shed postmortemly, or being juvenile they have not yet erupted, or being gerontic they have been lost. The nature of the material being what it is, it is difficult to decide which explanation best fits each case. Sectioning through the alveolar region is not always possible in order to base a count on the nature of the alveoli. The usual number of incisors is 5 but in some forms it is 4 or even 3. Can the number be considered a character of systematic value? If the juvenile and mature incisors are of the same size then obviously the premaxilla of a young animal could only house a smaller number than that of the mature animal. In using the number of incisor teeth as a taxonomic character the age of the animal must thus be taken into account.

The number of postcanine teeth in the Titanosuchians varies greatly, from 1 to 19, and is of doubtful systematic value. In some, these teeth are small; in others, strong; in some specimens they are regularly spaced and in others quite irregular. The two sides are often dissimilar, e.g. in *Enobius* there are, according to Broom, in the left dentary '. . . portions of three molars. There certainly have been four, and very probably there have been five', and on the right side

Broom found only one tooth behind the canine. In general it can be stated that in the Jonkerias the postcanines are regularly spaced and form a long series, whereas in the Anteosaurians they are irregular and the series is short.

With the material at my disposal I can state that the dentary usually has one incisor less than the corresponding premaxilla. It would also appear that there are fewer postcanines in the dentary than in the opposing maxilla.

Teeth on the palatines occur in the Anteosaurians and in the fragment called *Scullya*, but have as yet not been recorded in the Jonkerias although I found some indication in *Jonkeria ingens* (A.M.N.H. No. 5608).* These teeth are mostly seen only in section but in S.A.M. No. 11592 there is preserved a small pointed tooth slightly recurved. In the Anteosaurians the palatine teeth are situated on a prominent elevation, semilunar or reniform in shape. Their function seems clear—the incisors and canines tear out a lump of flesh from the victim and this is then held by the raised palatine teeth as an intermediate stage in the swallowing process. The palatine teeth situated on this characteristic boss constitute a diagnostic character of value.

Key for the Genera

Bearing the above remarks in mind we may now proceed with our attempt to arrange the Titanosuchians in some reasonable order. As a preliminary step, and in practice of considerable value, to facilitate the process of a rough-and-ready sorting out of the 14 genera, I propose making use of the following key:

A. Forms without bosses on postorbital bar and angular, incisors not long and with step:
   1. With many regular postcanines, no palatine boss—*Jonkeria*, *Dinosphageus*, *Dinopolus*.
   2. With few postcanines—*Dinartamus*.

B. Forms with bosses on postorbital bar and angular, incisors long and without step:
   3. With variable irregular postcanines, prominent palatine boss—*Anteosaurus*, *Dinosuchus*.
   4. With variable irregular postcanines, probably with palatine boss—*Titanosuchus*, *Scapanodon*, *Archeosuchus*, *Lamiasaurus* (snout), *Dinocynodon*, *Scullya*, *Titanognathus*, *Enobius*.

Redefinition of Genera

With our increased knowledge of the Titanosuchians it has become advisable to redefine the valid genera:

* For the institutions housing the specimens here referred to the following abbreviations are used: A.M.N.H., American Museum of Natural History, New York. S.A.M., South African Museum, Cape Town. B.M., British Museum (Natural History), London. T.M., Transvaal Museum, Pretoria. A.K., Alte Akademie, Munich. K.M., Kimberley Museum, Kimberley.

I. *Jonkeria* van Hoepen 1916.

The genotype *J. truculenta* is based upon an excellent skull and lower jaw.

1. Skull size—this is medium to large, not massive.
2. Bosses—there are no prominent bosses.
3. Additional pachyostosis—the parietals form a prominent ridge thickened round the pineal foramen but do not form a well-demarcated boss.
4. Palatine—there is no prominent boss, but the palatine is possibly dentigerous.
5. Premaxilla—the dentigerous border does not curve upwards and there is also no corresponding upward sweep of the dentary.
6. Incisors—are of medium length with labial talon pointed and with well-developed lingual crushing surface.
7. Pineal foramen—penetrates anterior part of the parietals and is thus some distance from the occipital border.
8. Snout—is relatively long, broader than high, the frontals are only slightly swollen, the premaxilla is fairly flat.
9. Squamosal—does not extend far ventrally and does not sweep far posteriorly, posterior to the interparietal. There is also little lateral sweep of the squamosal.
10. Temporal fossa—this is fairly large, with the antero-posterior and dorso-ventral diameters moderate and approximately equal, not extending much laterally, as the squamosal does not sweep much outwards.
11. Intertemporal width—this is small to moderate; the parietals are laterally pinched in to form a fairly high and narrow parietal crest.
12. Dentary—this is strong but not massive, with sloping mentum.
13. Dental formula—i.$\frac{4-5}{4}$, c.$\frac{1}{1}$, p.c $\frac{14-19}{13-15+}$.

Synonym. As thus defined *Dinosphageus* and *Dinopolus* become congeneric with *Jonkeria*.

II. *Anteosaurus* Watson 1921.

The genotype, *A. magnificus*, is based upon the major portion of a skull somewhat weathered.

1. Skull size—this is small to very large, slightly to very massive.
2. Bosses—a medium to very prominent boss is present on the dorsal part of the postorbital bar, and there is a prominent oval boss on the angular, the boss on the jugal is absent or low and moundlike to very prominent.
3. Additional pachyostosis—the parietals are much thickened but do not form a crest, greatly thickened around the pineal foramen to form a mound or well-demarcated circular boss; the frontals are greatly thickened to produce a medium to very prominent swelling.

4. Palatine—there is a prominent semilunar ridge-like or reniform boss-like eminence carrying irregular small pointed teeth.
5. Premaxilla—the dentigerous border curves antero-dorsally to form an obtuse angle with the maxillary border and there is little corresponding upward sweep of the anterior part of the dentary.
6. Incisors—are long to very long, the labial talon forming most or all of the tooth, with the lingual crushing surface greatly reduced to form little more than a cingulum, or are altogether absent.
7. Pineal foramen—penetrates the posterior part of the parietals and is thus near the occipital border.
8. Snout—is of medium length, higher than broad, the frontals are greatly swollen, the premaxilla is dorsally swollen and demarcated from the maxilla by a groove.
9. Squamosal—extends moderately to far ventrally and sweeps far posteriorly, i.e. much posterior to the occipital surface of the interparietal, and sweeps far to very far outwards.
10. Temporal fossa—this is large, with the dorso-ventral diameter greater than the antero-posterior, extending much laterally due to the outward sweep of the squamosal.
11. Intertemporal width—this is moderate to large, the parietals are laterally somewhat pinched in, but do not form a high and narrow crest.
12. Dentary—this is strong and fairly to very massive, with fairly upright mentum.
13. Dental formula—i.$\frac{3-5}{3-4}$, c.$\frac{1}{1}$, p.c.$\frac{5-15?}{5-?}$

Synonyms. As thus defined *Dinosuchus* becomes congeneric with *Anteosaurus*.

III. *Dinartamus* Broom 1923.

The genotype, *D. vanderbyli*, is based upon portions of a skull, probably associated.

1. Skull size—this is probably large, not massive.
2. Bosses—no evidence is preserved.
3. Additional pachyostosis—no evidence of this is preserved.
4. Palatine—no evidence of a palatine boss is preserved.
5. Premaxilla—the border does not curve upwards.
6. Incisors—according to Broom, 'the first is of Deinocephalian type, but the other three incisors may have had pointed crowns. There is some little indication that this may have been so.'
7. Pineal foramen—this area is not preserved.
8. Snout—this is weathered.
9. Squamosal—this is not preserved.
10. Temporal fossa—this region is not preserved.
11. Intertemporal width—this region is not preserved.

12. Dentary—in the associated specimen the dentary is apparently fairly massive with a fairly upright mentum.
13. Dental formula—according to Broom, i.$\frac{4}{3}$, c.$\frac{1}{1}$, p.c.$\frac{5}{5}$.

IV. *Titanosuchus* Owen 1879.

The genotype, *T. ferox*, is based upon upper and lower jaw fragments showing sections of the teeth roots. The only diagnostic features that can be determined in the genotype are: dentary strong and massive with mentum apparently fairly upright, and dental formula: i.$\frac{5}{4}$, c.$\frac{1}{1}$, p.c.$\frac{11}{10\text{-}11}$.

Other forms considered here are:

Titanosuchus cloetei (Broom 1903) is based on a piece of massive dentary, with the incisors lacking a lingual crushing surface and with the dental formula: i. 4, c. 1, p.c. 4+.

Scapanodon (Broom 1904). The type species is based upon two imperfect, badly preserved jaws showing a series of teeth: i. 2+, c. 1, p.c. 11+.

Archaeosuchus (Broom 1905). The type of the type species is a partial maxilla with some teeth; according to Broom c. 1, p.c. 8 (in 1932 Broom gives 7 postcanines).

Lamiasaurus (Watson 1914). Only the snout is considered here. The premaxillary border is not dorsally directed and the dental formula is i. 4 or 5, c. 1, p.c. 3–4.

Dinocynodon (Broom 1929). For the type dentary Haughton (1915) states that the symphysis is massive and square, and the dental formula is i. 4, c. 1, p.c. 11+, and Broom gives as the only generic character 'the extreme flattening of the large canine'. Now, in a specimen of *Anteosaurus*, there is a canine on the point of being shed which is also flattened, and this character can thus hardly be considered of generic value.

Scullya (Broom 1929). The type species is based upon 'a very badly crushed snout' with the dental formula i. 5, c. 1, p.c. 12, and the only other characters are the possible presence of teeth on the palatine and the dentary massive.

Titanognathus (Broili and Schröder 1935). The type of the type species consists of skull fragments showing, 'Schädel mit schmaler und steil vom prämaxillaren Kieferrand aufsteigender Schnauze, sehr gross. Praemaxillarer Kieferrand gegenüber dem maxillarer stark in die Höhe gezogen, Symphysenregion des Unterkiefers entsprechend erhöht gegenüber dem rückwartigen Abschnitt des Dentale. Zahnformel: i. $\frac{5}{4(?)}$ c. $\frac{1}{1}$, p.c. $\frac{6}{+3?}$'.

Enobius (Broom 1923). The type of the type species consists of two dentaries; mentum massive and squarish, with the dental formula c. 1, p.c. 1–5.

From the above it is quite evident that this series of fragmentary 'types' affords no very trustworthy bases on which they can be distinguished from

each other generically. I propose lumping all these forms together and to redefine the genus *Titanosuchus* compositely as follows:

1. Skull size—this is very probably large and massive.
2. Bosses—are probably present.
3. Additional pachyostosis—of this no evidence is preserved.
4. Palatine—this is not preserved.
5. Premaxilla—the dentigerous border curves antero-dorsally with an associated step-up of the anterior part of the alveolar border of the dentary.
6. Incisors—these are apparently long, with no lingual crushing surface.
7. Pineal foramen—no evidence is preserved.
8. Snout—is probably as in *Anteosaurus*.
9. Squamosal—is not preserved.
10. Temporal fossa—this area is unknown.
11. Intertemporal width—this area is not preserved.
12. Dentary—this is strong and massive with a squarish and upright mentum.
13. Dental formula: i. $\frac{4-5}{4}$, c. $\frac{1}{1}$, p.c. $\frac{11-15+}{7-12+}$.

Synonyms: *Scapanodon*, *Archaeosuchus*, *Lamiasaurus* (snout), *Dinocynodon*, *Scullya*, *Enobius*, and *Titanognathus*.

The Specific Names of the Above Forms

Until a detailed study is completed it is impossible to make any statement on the validity of the specific names given by authors. Meanwhile a list is appended of the names as they stand at the present moment in the literature, but under the genera—*Anteosaurus*, *Dinartamus*, *Jonkeria* and *Titanosuchus*—as defined above.

Genus *Anteosaurus:*

A. abeli Boonstra 1952. Plates I–V and IX.

Type. A good skull and lower jaw. S.A.M. No. 11296.

A. magnificus Watson 1921.

Type. Major part of skull. B.M. No. 3595.

A. minor (Broom) 1929.

Type. Fragment of skull. B.M. No. 5742.

Referred specimens:

S.A.M. No. 11492. A somewhat weathered skull.

S.A.M. No. 11694. A good skull. (Plate VI, figs. 1, 2.)

Additional diagnostic features revealed by these two skulls are: In S.A.M. No. 11492, the left premaxilla has no incisors preserved, but on the right side there are three incisors, fairly long, with no indication of a lingual step; in S.A.M. No. 11694 no incisors are present, the dentigerous boss on the palatine is prominent and semilunar in outline; there is no indication of a jugal boss. The dental formula is i. 0–3, c. 1, p.c. 7–8.

A. vorsteri (Broom) 1936.
Type. A good skull. T.M. 265, Broom's *Dinosuchus vorsteri.*
Referred specimen: a good skull. S.A.M. No. 11577. (Plates VII and VIII.)

Genus *Dinartamus:*

D. vanderbyli Broom 1923.
Type. Skull fragments. Coll. Broom.

Genus *Jonkeria:*

J. angusticeps (Broom) 1929.
Type. Good lower jaw. A.M.N.H. No. 5633. Broom's *Phoneosuchus angusticeps.*

J. haughtoni (Broom) 1939.
Type. Fairly good skull. S.A.M. No. 4343. Broom's *Dinosphageus haughtoni.*

J. ingens (Broom) 1923.
Type. Fair skull. A.M.N.H. No. 5634. Broom's *Dinophoneus ingens.*
Synonym. *J. pugnax* (Broom) 1929. Fairly good skull and lower jaw. A.M.N.H. No. 5608.

J. truculenta van Hoepen 1916.
Type. Good skull and lower jaw. T.M. 212.

J. vanderbyli (Broom) 1929.
Type. Good skull. A.M.N.H. No. 5620.

J. spp. The lack of identifiable cranial elements makes the specific status of *J. crassus* (Broom) 1929, Type A.M.N.H. No. 5577, uncertain. The skull referred to *Scapanodon duplessisi* by Broom 1923 is undoubtedly a *Jonkeria* species. Further study may prove synonomy with one of the named species and until then it is best left unnamed. *Dinopolus atrox* Broom 1923, Type T.M. 274, consists of a snout. The incisors are short, the anterior three with ledge, the outer without ledge, according to Broom. The lower canine peculiar, but otherwise it falls under *Jonkeria* as here defined. These characters may indicate that it is a distinct species—*Jonkeria atrox* Broom, bridging the gap between *Dinartamus* and *Jonkeria.*

Genus *Titanosuchus:*

T. cloetei (Broom) 1903.
Type. Piece of dentary. S.A.M. No. 731.

T. dubius (Haughton) 1915.
Type. Major part of dentaries. S.A.M. No. 2759. Broom's *Dinocynodon dubius.*

T. ferox Owen 1879.
Type. Upper and lower jaw fragments. B.M. No. 49370.

T. gigas (Broom) 1929.
Type. A very badly crushed snout. Coll. Broom. Broom's *Scullya gigas.*

T. lotzi (Broili and Schröder) 1936.

Type. Skull fragments. A.K. (no number given). Broili and Schröder's *Titanognathus lotzi*.

T. strubeni (Broom) 1923.

Type. Partial dentaries. K.M. (no number given). Broom's *Enobius strubeni*.

Incertae sedis. The following forms do not merit separate generic rank and may best be regarded as species of *Titanosuchus*, whose specific validity is questionable.

T. duplessisi (Broom) 1904.

Type. Imperfect badly preserved jaws. S.A.M. No. 769. Broom's *Scapanodon duplessisi*.

T. cairncrossi (Broom) 1905.

Type. Part of maxilla. S.A.M. No. 916. Broom's *Archaeosuchus cairncrossi*.

T. newtoni (Watson) 1914.

Type. Snout. B.M. No. 49385. Watson's *Lamiasaurus newtoni*.

REFERENCES

Boonstra, L. D. 'A note on the synonymy of the two deinocephalians, *Dinophoneus ingens* Broom and *Jonkeria pugnax* (Broom).' *S. Afr. J. Sci.*, vol. 32, pp. 329–31. 1935.

'The cranial morphology of some titanosuchid deinocephalians.' *Bull. Amer. Mus. Nat. Hist.*, vol. 72, pp. 99–116, pls. 9–17. 1936.

Miljoene Jare Gelede in die Karoo. Johannesburg, Voortrekkerpers, 125 pp. 1948.

''n Nuwe Titanosuchiërsoort (*Anteosaurus abeli*).' *Tydsk. Wet. en Kuns*, xii, bls. 142–9. 1952.

Broom, R. 'On evidence of a new species of *Titanosuchus* (*T. cloetei*).' *Ann. S. Afr. Mus.*, vol. 4, pp. 142–3. 1903.

'Notice of a new fossil reptile (*Scapanodon Duplessisi*) from the lower Karroo beds of Prince Albert, Cape Colony.' *Rec. Albany Mus.*, vol. 1, pp. 182–3. 1904.

'Notice of some new fossil reptiles from the Karroo beds of South Africa.' ibid., vol. 1, pp. 331–9. 1905.

'A comparison of the Permian reptiles of North America with those of South Africa.' *Bull. Amer. Mus. Nat. Hist.*, vol. 28, pp. 197–234. 1910.

'On the structure of the skull in the carnivorous deinocephalian reptiles.' *Proc. Zool. Soc.* London, pp. 661–84. 1923.

'On the carnivorous mammal-like reptiles of the family Titanosuchidae.' *Ann. Transvaal Mus.*, vol. 13, pp. 9–36, pl. 4. 1929.

The mammal-like reptiles of South Africa and the origin of mammals. London, H. G. and G. Witherby, xvi. pp. 376. 1932.

'On some new genera and species of Karroo fossil reptiles, with notes on some others.' *Ann. Transvaal Mus.*, vol. 18, pp. 349–86. 1936*a*.

'On the structure of the skull in a new type of dinocephalian reptile.' *Proc. Zool. Soc.* London, pp. 733–42. 1936*b*.

Broili, F., and Schröder, J. 'Ein Dinocephalen-Rest aus den unteren Beaufort-Schichten.' *Sitzber. Bayrischen Akad. Wiss.*, pp. 93–114. 1935.

Gregory, W. K. 'The skeleton of *Moschops capensis* Broom, a dinocephalian reptile from the Permian of South Africa.' *Bull. Amer. Mus. Nat. Hist.*, vol. 56, pp. 179–251, pls. 1–21. 1926.

Haughton, S. H. 'On two new therocephalians from the Gouph.' *Ann. S. Afr. Mus.*, vol. 12, pp. 55–7. 1915.

Hoepen, E. C. N. van. 'A new Karroo reptile.' *Ann. Transvaal Mus.*, vol. 5, suppl. 3, no. 3, 1 p. 1916.

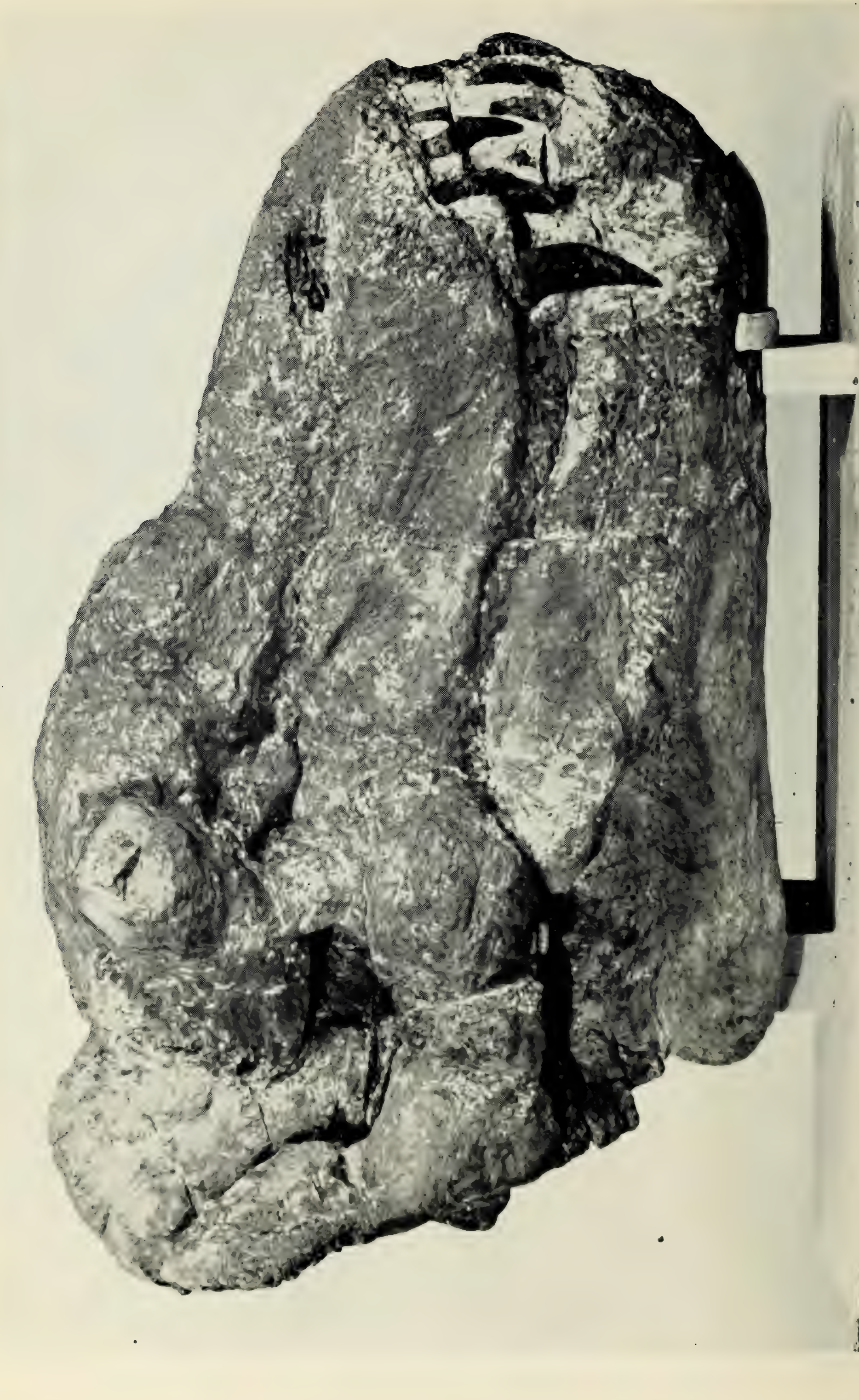
Owen, R. 'Description of fragmentary indications of a huge kind of theriodont reptile (*Titanosuchus ferox Ow.*) from Beaufort West, Gough Tract, Cape of Good Hope.' *Quart. Jour. Geol. Soc.*, vol. 35, pp. 189–99, pl. 11. 1879.

Watson, D. M. S. 'The Deinocephalia, an order of mammal-like reptiles.' *Proc. Zool. Soc.* London, pp. 749–86, pls. 4, 5. 1914.

'The bases of classification of the Theriodontia.' ibid., pp. 35–98. 1921.

[*Photos: G. R. McManus*

Anteosaurus abeli Boonstra. Type specimen. S.A.M. No. 11296. Lateral view, about ¼ natural size.



Anteosaurus abeli Boonstra. Co-type. S.A.M. No. 9329. Lateral view, about ¼ natural size. Angle of lower jaw restored.

Anteosaurus abeli Boonstra. Co-type. S.A.M. No. 4340. Lateral view, about ½ natural size.

Anteosaurus abeli Boonstra. Co-type. S.A.M. No. 11293. Latera view, about ¼ natural size. Anterior part of snout restored.

Anteosaurus abeli Boonstra. Co-type. S.A.M. No. 11293. Dorsal view, about $\frac{1}{4}$ natural size. Anterior part of snout restored.

Anteosaurus minor (Broom). Referred specimen. S.A.M. No. 11694. About $\frac{1}{4}$ natural size. Fig. 1, lateral view. Fig. 2, ventral view.

Anteosaurus vorsteri (Broom). Referred specimen. S.A.M. No. 11577. Lateral view, about ¼ natural size.

Anteosaurus vorsteri (Broom). Referred specimen. S.A.M. No. 11577. Dorsal view, about ¼ natural size.

Anteosaurus abeli Boonstra. Photograph of life-size reconstruction in plaster of the head, based on the skulls of the type and co-types figured in the foregoing plates. (Nasionale Pers photo.)

4. *The Gorgonopsians,* Aelurognathus microdon *and* Hipposaurus boonstrai, *reconstructed.* By L. D. Boonstra, D.Sc.

(With Plates X–XVI)

In 1934 I described a new species of Gorgonopsian under the name *Aelurognathus microdon.* The specimen consisted of a skull, much of the vertebral column, an excellent pectoral girdle, a good fore-limb with most of the carpus, a good pelvis and most of the hind-limb. (Plate X.)

The fragile nature of the preserved bones has made it impossible to attempt a free mount of the skeleton as preserved. During 1937 Mr. J. Drury, then modeller to the South African Museum, modelled in plaster of paris all the elements preserved, two-thirds natural size. Utilizing our knowledge derived from other gorgonopsians species (see op. cit.) the missing bones were restored.

The resulting mount could be considered fairly accurate and a photograph of it was published in the 'Report of the South African Museum for 1937' and republished in a popular booklet *Miljoene Jare Gelede in die Karoo.* Apparently both these have passed unnoticed by overseas colleagues, and Colbert in his study of *Lycaenops ornatus* does not mention either of these publications.

An augmented set of new photographs of the modelled skeleton (Plates XI–XIII) and of the animal reconstructed 'in the flesh' (Plate XIV), also by Drury, is here presented for comparison with the excellent set of photographs published by Colbert of the remarkable free-mount of *Lycaenops ornatus* as mounted by Charles Lamb after preparation by Jeremiah Walsh.

Aelurognathus microdon has been reconstructed with 29 presacral vertebrae (including the proatlas) measuring 750 mm.; 3 sacrals (90 mm.); 29 caudals (585 mm.). All these measurements are projections. The total projected length of the skeleton is 1,530 mm. and measured over the curvature of the back is 1,650 mm. The shoulder height is 570 mm. and at the hips the height is 368 mm.

The Stance of Aelurognathus

The following remarks should be read in conjunction with the section in Colbert's paper, 'The Skeleton as a Whole', as, after his masterly account, written with the help derived from Schaeffer's movie-film of the alligator, I can here be brief and confine myself to the conditions in *Aelurognathus* without repetition of comparisons with other Therapsids.

Drury's model is mounted showing *Aelurognathus* in the standing position based on views held in 1937, some of which have since been modified necessitating some alterations to the original mount. (Plate XIV.)

The curvature of the spine, as mounted, is probably over-accentuated with the apex of the curve too far forward and I now think that in life the back

would have been much straighter with the curve nearer the sacrum. In this I would be in agreement with Colbert.

The ribs form a complete presacral set. On this point I had in 1937 corrected the erroneous view expressed in 1934 as to the probable absence of lumbar ribs in *Lycaenops*, thereby anticipating Colbert's criticism of 1948 and thus admitting its validity in advance.

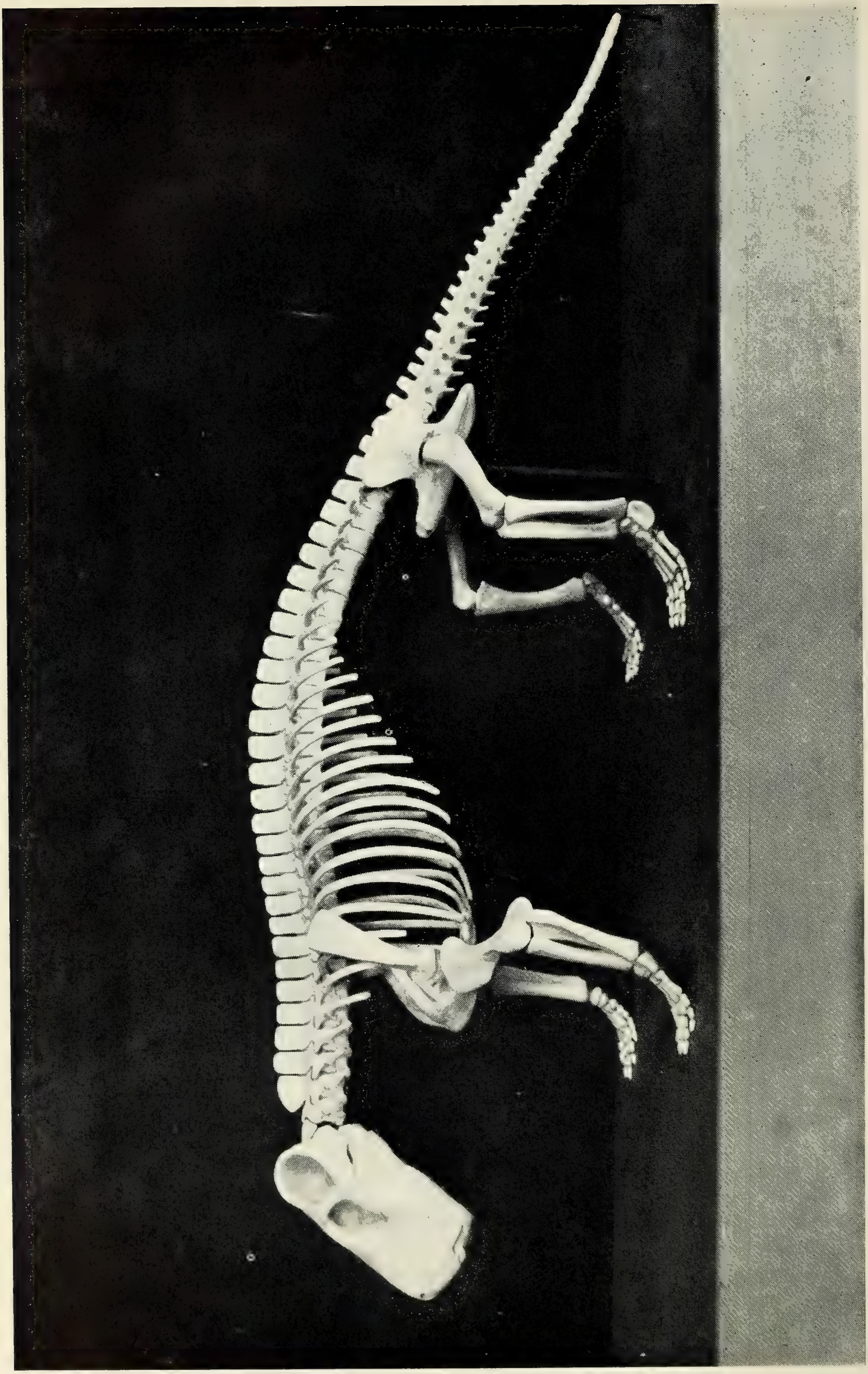
The skull hangs downward, dog-fashion, and, in harmony with this, I would now prefer the neck to show a more pronounced downward curve.

The pectoral girdle was preserved in approximately natural articulation and this position is retained with little correction in the model. As mounted *Aelurognathus* has a deep chest—much deeper than *Lycaenops* as shown in Colbert's figure 22. In lateral view the scapula has a slight backward tilt when the animal is in the standing position. When executing a stride, the forward side would show the scapula tilting further backwards with its posterior edge everted, i.e. there would be some rotation of the scapula on its long axis. In anterior view the scapular girdle is V-shaped, but, with the scapular blade somewhat curved, the top edge with the cartilaginous suprascapula would not stand excessively away from the ribs. This I believe to be the natural position of the pectoral girdle, for in this position the glenoid articulation would appear to function properly. When executing a stride the left humerus would, in the forward position, be directed somewhat laterally, and the right humerus be directed backwards close in to the body. To keep both the humeri in articulation the direction in which the glenoids face must be in keeping. This would be achieved by a lateral sigmoidal curvature of the spine accompanied by a slight movement of the scapular girdle as a whole, and also of its two halves individually, in relation to the clavicular girdle. Thus the left half of the scapular girdle would move forwards, sag slightly and rotate on its long axis so that the glenoid is directed more outwards and, at the same time, the right half would concomitantly rotate so that the right glenoid is directed slightly inwards from the backwardly facing position.

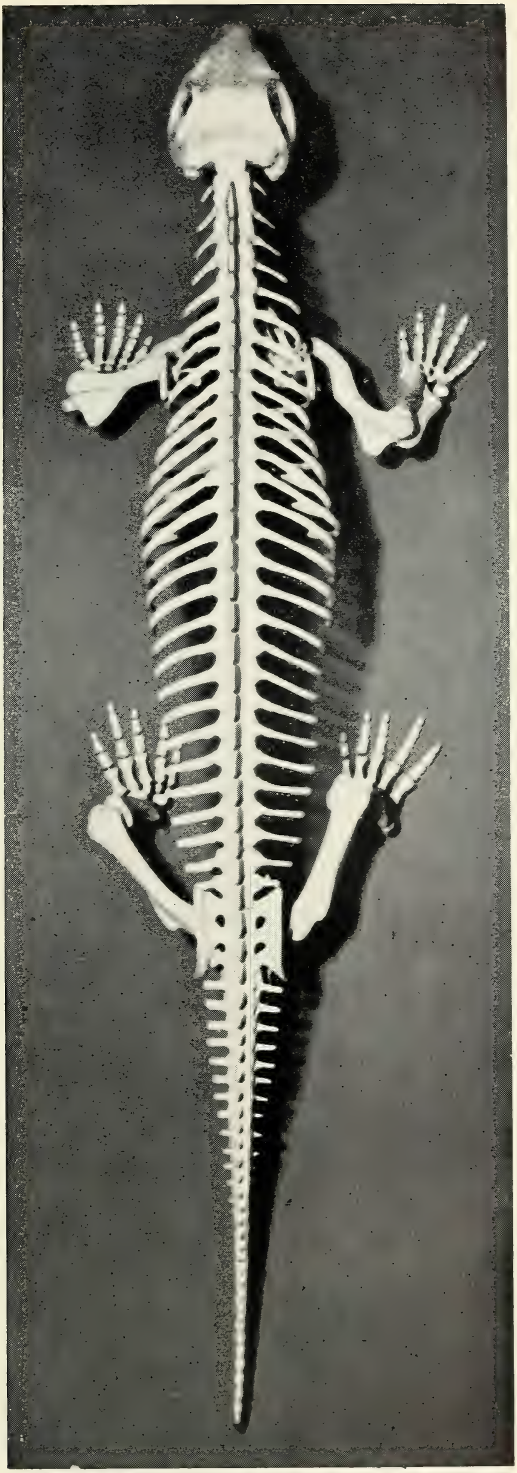
In the mount, with the animal in the standing position, i.e. nearly half-way through the stride, the humerus is directed obliquely outwards with the distal end appreciably lower than the proximal end, and the elbow is thus everted but less anteriorly and downwardly directed than would be the case at the commencement of the stride.

The femur, in the 1937 mount, is directed obliquely forward and outward with the distal end much lower than the acetabulum. I now think that the femur was too much everted and that in life the knee would be closer in to the body. This correction has now been made to the mount as shown in the accompanying new photographs—on the right side the femur is brought in closer to the body than the left side. In the stride of the back limbs the spine would be flexed in the lumbar region to complete the sigmoid curve which the movement of the fore-limbs initiated.

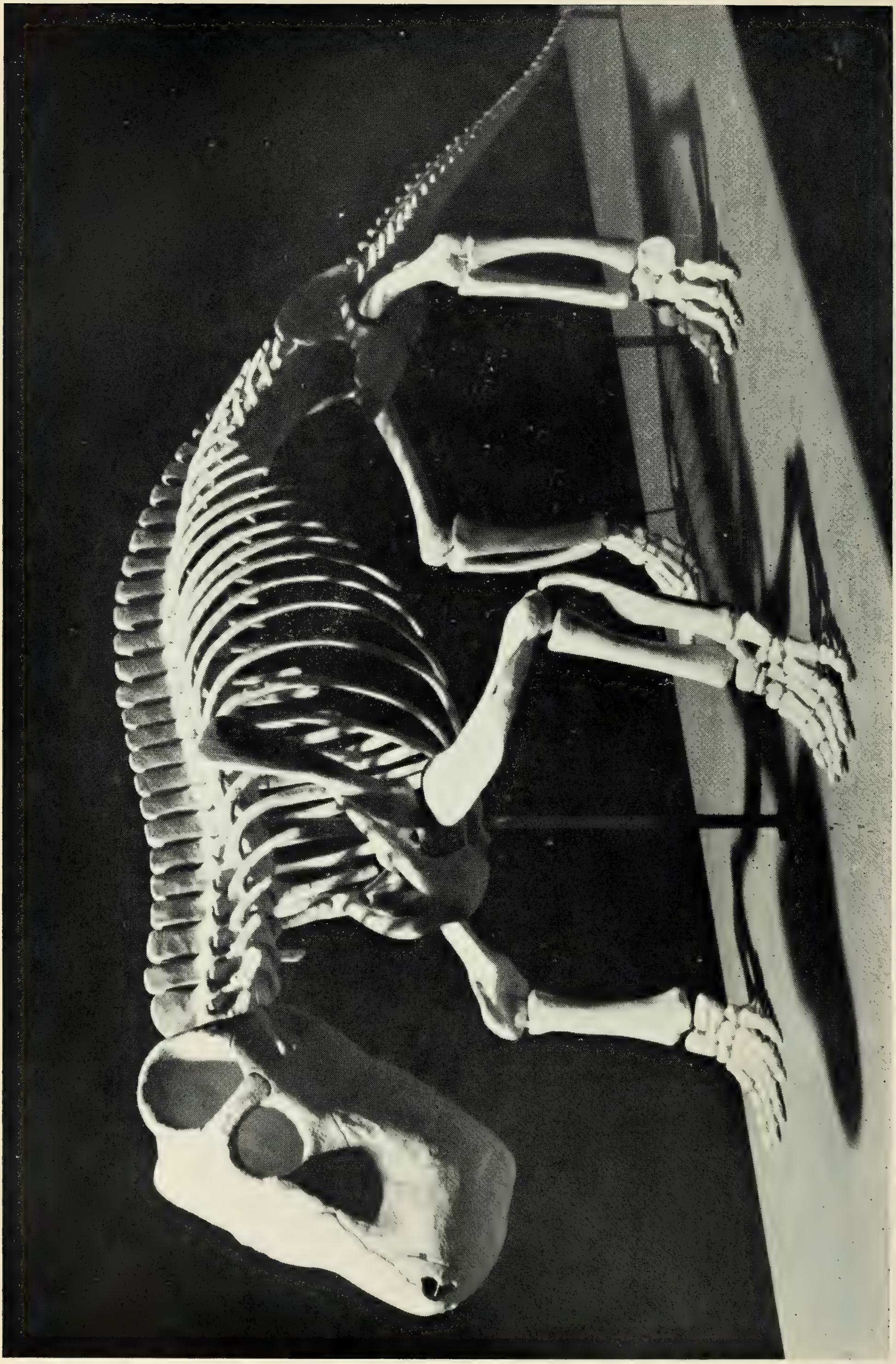
Skeleton of *Aelurognathus microdon* laid out in the *in situ* position. About $\frac{1}{6}$ natural size. S.A.M. No. 9344.



Modelled skeleton of *Aelurognathus microdon*. Lateral view, about $\frac{1}{8}$ natural size.



Modelled skeleton of *Aelurognathus microdon*. Dorsal view, about $\frac{1}{8}$ natural size.



Modelled skeleton of *Aelurognathus microdon*. Oblique view.

Model of *Aelurognathus microdon* 'in the flesh' by J. Drury (South African Museum).

Hipposaurus boonstrai modelled natural size in plaster-of-paris by the author. Photo about $\frac{1}{6}$ natural size.

Hipposaurus boonstrai. Oblique view of the above reconstruction.
All photographs by Nasionale Pers, Cape Town

In the reconstruction the feet are probably mounted slightly too much in the semi-digitigrade position. They should, in the standing position, be more plantigrade. At the commencement of the stride they would be wholly plantigrade, and, at the completion of the stride, the digitigrade position would be obtained just before the foot is lifted from the ground. The fore-feet are correctly shown as forwardly directed, and, with the knees drawn in to the body in the corrected mount, the hind-feet also assume a more natural forward position than was the case in the 1937 mount.

For comparison I have included here some hitherto unpublished photographs of a life-sized reconstruction of *Hipposaurus boonstrai* which I have myself modelled in plaster, with due acknowledgment to Colbert for ideas derived from his *Lycaenops* paper. (Plates XV and XVI.)

Hipposaurus is here represented in the walking position and the greater straightness of the back is noteworthy. The right fore-foot, at the commencement of the stride, is flat on the ground; the left, nearly at the completion of the move, is semi-digitigrade. The left hind-foot, just after the commencement of the stride, is semi-plantigrade with the knee probably everted a little too far; the right hind-foot is just about to be lifted and swung forwards after having completed the stride.

REFERENCES

Boonstra, L. D. 'A Contribution to the Morphology of the Gorgonopsia.' *Ann. S. Afr. Mus.* 31, p. 137. 1934.
Report of the South African Museum for 1937, p. 9 and plate facing p. 18. 1938.
Miljoene Jare Gelede in die Karoo. Voortrekkerpers, Johannesburg. p. 51. 1948.
'Bewoners van die Oer-Karoo', *Die Huisgenoot,* Cape Town, 6 Aug., p. 23. 1948.
'Wêreld van 250 Miljoen Jaar Gelede.' *Die Burger,* Cape Town, 11 May, p. 3. 1950.
Bystrow, A. P. 'Rekonstuktionversuche einiger Vertreter der Nord-Dwina Fauna.' *Akad. Nauck,* U.S.S.R., 4, p. 289. 1935.
Colbert, E. H. 'The Mammal-like Reptile, *Lycaenops*.' *Bull. Am. Mus. Nat. Hist.,* 89, 6, p. 357. 1948.

5. *The cranial morphology and taxonomy of the Tapinocephalid genus* Struthiocephalus.

By L. D. Boonstra, D.Sc.

(With Plate XVII and 6 text-figures)

The one important genus of the Tapinocephalid Deinocephalians[1] of which the cranial structure has hitherto not been adequately described is *Struthiocephalus.*

Up to date five species of *Struthiocephalus* have been created. Few details of the cranial structure were published before I re-examined the type skull[2] and described the two new species, *duplessisi*[3] (since transferred to the new genus *Struthiocephaloides*[8]) and *akraalensis*.[4] Of Broom's *rheederi*[5] and Olson and Broom's *milleri*[6] little more is known than can be gathered from Broom's sketches of the outlines of the skull and the main skull openings—temporal fossae, orbits, nostrils and the pineal foramen.

In the collection of the South African Museum there is, besides the type skulls of *whaitsi* (S.A.M. 2678), and *akraalensis* (S.A.M. 3719), an excellently preserved skull of the species *whaitsi* (S.A.M. 11591) showing nearly all the features of the dorsal, lateral, occipital and palatal surfaces and the right side of the brain-case, and a juvenile skull (S.A.M. 11493) of the same species. The skull of the mounted specimen which has associated with it much of the postcranial skeleton (S.A.M. 3012) is crushed and shows little of the detailed structure.[7]

The structural details determined in these five specimens are here pooled to give an account of the cranial morphology of the genus but the figures are all of the one specimen of *whaitsi* (S.A.M. 11591).

The General Shape and Form

The generic name very aptly describes the shape of the skull as being very similar to the shape of the head of an ostrich. Anterior to the orbital border the snout is anteriorly directed, long, shallow but fairly broad and, in relation to the part of the skull posterior to the orbits, appears weak. With the lower jaw occluded the muzzle appears much less weak as the mentum is quite massive. The skull is low—the width over the quadratojugals being much greater than the height in this plane. The bones of the posterior part of the skull are all strongly pachyostosed, whereas those of the snout are only relatively moderately thickened with the outer bone surface smooth. The transition from the posterior part of the dorsal surface to the dorsal and lateral surface of the snout is thus abrupt but less abrupt than in *Mormosaurus*. As the strong pachyostosis does not include the lacrimal and only affects the posterior part of the prefrontal the transition from the smooth snout to the rough posterior part lies further back than in *Taurocephalus* and *Mormosaurus*. The pachyostosis in *Struthiocephalus* is not general over the posterior part of the outer surface—the 'cheek' being still

fairly light and its surface smooth, and on the dorsal surface the strong thickening is still localized, emanating from distinct centres. The pachyostosis forms a strong rugose, dorsally somewhat bulbous, postorbital bar; a prominent rugose boss surrounding the pineal foramen and a peculiar naso-frontal boss. (The first is reminiscent of the condition in the Titanosuchid *Anteosaurus*, where it is very strongly developed, and the last a feature which it has in common with the Tapinocephalid *Keratocephalus*.)

The orbits, situated in the posterior half of the skull, are large, round and directed forwards and outwards with the thickened postero-dorsal half of the orbital border strongly overhanging.

The nostrils are large and elongated, situated on the dorsal surface mainly dorsally, and only slightly laterally directed and are well back from the anterior edge of the snout, close to each other and separated by a strong internasal bar.

The temporal fossa is fairly large, higher than long, and the pachyostosis of the postorbital bar and the posttemporal arch has not reduced its size much; its anterio-posterior diameter is still greater than in *Mormosaurus* and much greater than in the slitlike fossa of *Tapinocephalus*. Dorsally, it extends medially to form a bay encroaching into the parietal region (in *akraalensis* the fossa approaches the condition in *Mormosaurus*).

The interparietal width is moderate, due to a pinching-in laterally of the parietals to form the dorso-median bay of the temporal fossa.

Due to the forward position of the quadrate, which lies anterior to the plane of the orbit, the lower jaw is short and the maximum gape of the jaws is comparatively small.

The anterior teeth of the upper jaw are directed much anteriorly but the intermeshing teeth of the dentary are directed dorsally.

The Bones of the Dorsal and Lateral Surfaces (figs. 1 and 2)

The matrix of the *Tapinocephalus*-zone being notoriously intractable, the determination of sutures in most specimens from this horizon is extremely difficult. Thus Haughton in his description of *S. whaitsi* and Broom in the case of *S. rheederi* and Olson and Broom in *S. milleri* have, together, only figured parts of two sutures. It has only been through a laborious process of 'artificial weathering' by dilute hydrochloric acid that I have been able to determine most of the sutures, but some still remain indeterminable and others uncertain.

The premaxillaries (P.Mx.) together form a large part of the snout. From the anterior border they stretch posteriorly to past the middle of the skull. From its anterior border each premaxilla narrows, where it forms the inner border of the nostril, then it stretches as a long tapering bone posteriorly, where it lies in a groove of the nasals.

The nasals (N.) are long, narrow bones, which in their postero-median part are grooved to house the posterior tongue of the premaxillaries; posterior to the limits of the premaxillaries they meet on the dorsal surface in the median

line and are here thickened to form the anterior and major part of the naso-frontal boss.

The septomaxillaries (S.Mx.) appear to be small splint-like bones forming the outer border of the nostrils, but their limits are uncertain in most specimens.

The maxillaries (Mx.) are the largest bones of the snout, being long but shallow. Posteriorly a dorsal prong just meets the prefrontal, but in some specimens the lacrimal is intercalated, and a ventral prong extends far posteriorly with its upper edge applied to the lower border of the jugal. In between these two prongs lie the anterior ends of the lacrimal and jugal.

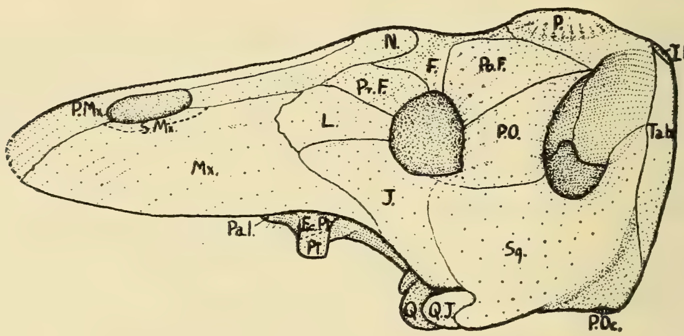


Fig. 1. *Struthiocephalus whaitsi*. Lateral view of the skull (S.A.M. 11591) (× ⅛). All the figures are not perspective drawings but projections drawn with the aid of a pantograph. The lateral view of the skull and that of the braincase are projected on to the median (sagittal) plane, the dorsal and ventral views are projected on to the plane of the alveolar border, and the occipital view at right angles to the plane of the alveolar border.

The lacrimal (L.) ventrally meets the upper edge of the jugal in a straight suture and these two bones together extend anteriorly into the posterior fork of the maxilla. The lacrimal is in its anterior extent as in *Mormosaurus* and thus stretches much further anteriorly than it does in *Taurocephalus*. It forms only a small part of the relatively unthickened anterior orbital border. Dorsally the prefrontal does not, in S.A.M. 11591, altogether exclude the lacrimal from contact with the nasal; in the other specimens a tongue of the prefrontal is intercalated between the nasal and lacrimal. (In *Taurocephalus* the lacrimal does not meet the nasal, but in *Mormosaurus* it does.)

The jugal (J.) is a strong bone; like the bones of the snout it is not greatly thickened and its surface is not rugose but smooth. It forms the antero-ventral comparatively unthickened border of the orbit. It extends far ventrally as a tapering element to be separated (in S.A.M. 11591) from the quadratojugal by a narrow incisure. Anteriorly it stretches far as a prolongation, with the lacrimal, into the posterior fork of the maxilla. The posterior border forms a shallow curve and is thus not deeply indented by an anterior wedge of the squamosal as in *Mormosaurus* and *Taurocephalus*.

The prefrontal (Pr.F.) is much thickened along its lateral edge to form the antero-dorsal thick, rugose and rounded portion of the orbital border. In all the specimens, except S.A.M. 11591, it has an anterior tongue which separates the lacrimal from the nasal. It does not extend much posteriorly, but is thickest here. Medially it is thinner and there is thus a hollow between the thickened orbital border and the naso-frontal boss.

The frontal (F.) is a large element of the dorsal skull roof. Its median part is roughly rectangular and from here three tongues extend: one, anteriorly inter-

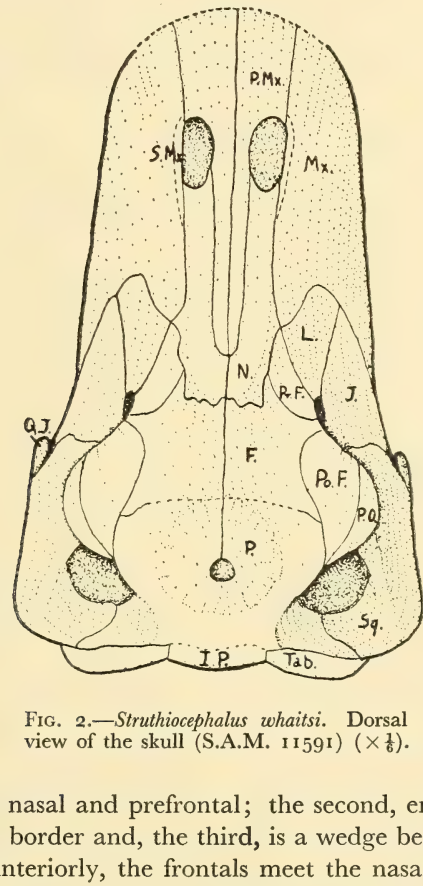


FIG. 2.—*Struthiocephalus whaitsi*. Dorsal view of the skull (S.A.M. 11591) (× ⅙).

calated between the nasal and prefrontal; the second, entering the thickened rugose upper orbital border and, the third, is a wedge between the postfrontal and the parietal. Anteriorly, the frontals meet the nasals and here form the posterior minor part of the naso-frontal boss. For the rest the frontals are not greatly pachyostosed and in *whaitsi* form a shallow saddle between the naso-frontal and parietal bosses, whereas in *akraalensis* the frontals are thickened in the median line with laterally a deep depression which is further laterally bounded by a strong ridge formed by the postfrontal and postorbital. Posteriorly, the frontals meet the parietals in a nearly straight frontal suture just anterior to the parietal boss surrounding the pineal foramen.

The postfrontal (Po.F.) forms the dorso-posterior corner of the orbital border which is here greatly thickened and very rugose. Its suture with the postorbital is in most specimens uncertain but in *whaitsi* (S.A.M. 11591) it is a large bone forming the dorsal swollen part of the postorbital bar, and in *akraalensis* it forms part of the ridge lying lateral to the depression in the surface of the frontal. This identification of the large size of the postfrontal in *Struthiocephalus* leads one to suspect that this element is a much larger bone than it has hitherto been thought to be in most Tapinocephalia. The pachyostosis of the postfrontal has resulted in the postorbital being practically excluded from the dorsal surface of the skull and thus forms only the lower part of the postorbital bar. Another result of the thickening of the postfrontal has been that together with the enlarged and thickened prefrontal the frontal tends to become excluded from the orbital border.

The parietals (P.) together form the greater part of the cranial roof. In their antero-median portion a large elevated and rugose boss is developed and is pierced by a large round pineal foramen. In their posterior half the parietals form a narrowed dorsal surface as they are here laterally pinched in. This pinching-in is less evident in *akraalensis*. Here a sharp edge separates the dorsal surface from a lateral surface, which forms the dorsal part of the median or inner face of the temporal fossa. This lateral parietal surface, extending on to the posttemporal arch to meet the squamosal, effectively prevents the postorbital from meeting the squamosal at this level. The medio-dorsal bay of the temporal fossa thus formed by the pinching-in of the parietals laterally is clearly shown in *whaitsi*, but in *akraalensis* the temporal fossa is more a continuous slit with this bay not clearly demarcated. Posteriorly, the parietals are buttressed by the interparietal in their median part and, more laterally, by the strong tabulars.

The postorbital (P.O.) is a massive element forming the lower part of the thickened postorbital bar which in its upper postfrontal part is bulbous on a scale just less than in the Titanosuchid *Anteosaurus*. The postorbital bar is strong, wide and fairly rugose in *whaitsi*, and very strong, very wide and strongly rugose in *akraalensis*. Posteriorly, the postero-lateral flange of the parietal lies between the posterior process of the postorbital and the squamosal. In a juvenile specimen of *whaitsi*, S.A.M. 11493, the posterior process of the postorbital still stretches far posteriorly, but even here does not meet the squamosal. Ventrally, the postorbital forms an overlapping suture with the squamosal.

The squamosal (Sq.) is the main constituent bone of the 'cheek'. It is a strong thickened element but, as in the jugal, its outer surface is not rugose but smooth in *whaitsi*, but with pits and rugae in *akraalensis*. Anteriorly, it meets the jugal in a long curved suture with no anterior wedge-shaped process as in *Mormosaurus* and *Taurocephalus*. Its postero-ventral corner overlaps on the outer surface of the quadratojugal. Dorsally, it is overlapped by the ventral edge of the postorbital, and, further, posteriorly, it forms the thickened lower border of the temporal fossa. From here it sweeps upwards to form most of the anterior

face of the posttemporal arch and here its dorsal end overlaps the postero-lateral flange of the parietal, where this bone forms the inner upper margin of the temporal fossa. Postero-ventrally, the squamosal forms the thickened rounded postero-ventral edge of the skull. This rounded border forms the lateral wall of the wide and deep auditory groove, which groove lies mostly in the squamosal. Medially to this groove, the squamosal forms a strong and prominent ridge, medio-ventrally buttressed by the paroccipital and further dorsally wholly formed by the tabular. This ridge, thus composed of squamosal, tabular and paroccipital, forms the median wall of the auditory groove and from it originated the strong depressor muscle of the mandible.

The tabular (Tab.) in dorsal view is seen to form the posterior half of the dorsal part of the posttemporal arch, supporting the anterior half formed by the flange of the parietal and the up-sweeping flange of the squamosal. In lateral view, the tabular is seen to form the lateral part of the posterior edge of the skull.

The interparietal (I.P.) in dorsal view, shows its upper edge where it forms the posterior buttress to the parietal in the median part of the posterior margin of the skull.

The quadratojugal (Q.J.) in dorsal and lateral views is seen to form the antero-ventral corner of the 'cheek'. Along its posterior border it is clasped by the squamosal and its inner surface supports the quadrate. Its dorsal margin does not abut against the jugal but is separated from it by a narrow incisure.

THE OCCIPUT (fig. 3)

The occiput in *Struthiocephalus* forms a large surface, much broader than high and nearly semicircular in outline. It is shallowly concave from side to side. In the median line it is nearly vertical with its dorsal edge slightly further posteriorly and here it lies in a plane nearly at right angles to the plane of the maxillary alveolar border. In the median line there is a ridge, which runs from the *foramen magnum* to the upper edge of the occipital surface. In *whaitsi* this ridge is wedge-shaped, broad dorsally and tapering to the upper edge of the *foramen magnum*, whereas in *akraalensis* this ridge is straight and narrow with a sharp edge forming the median line with a deep depression lateral to it. In this species the occiput has its ventral part situated much anteriorly so that it is no longer nearly at right angles to the alveolar border but forms an obtuse angle with the alveolar plane and an acute angle with the dorsal surface. This may be due to post-mortem dorso-ventral pressure.

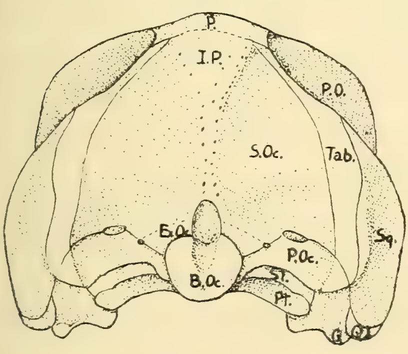


FIG. 3.—*Struthiocephalus whaitsi*. Occipital view of the skull (S.A.M. 11591) ($\times \frac{1}{6}$).

The condyle is directed postero-ventrally so that the skull would normally hang somewhat downwards. It forms a stout rounded knob, dorsally excavated by a groove leading into the *foramen magnum*. The *foramen magnum* is large and oval. The posttemporal fossae are small slits, bounded dorsally by the supraoccipital and ventrally by the paroccipital. The lateral outer border of the occipital plate is formed by the squamosal and median to this lies the deep auditory groove, whose inner wall is formed by a strong and prominent ridge to whose formation the tabular, squamosal and paroccipital contribute. Ventrally the condyles of the quadrates lie far anteriorly to the plane of the occiput. In occipital view the basioccipital condyle forms the median part of the ventral edge, and laterally the quadrate rami of the pterygoids together form a third of the ventral edge of the skull.

In only one specimen (S.A.M. 11591) is the occiput well preserved, and even here the sutures between the basioccipital and exoccipital and between the supraoccipital and interparietal cannot be determined.

The basioccipital (B.Oc.) apparently forms the whole of the condyle with no participation by the exoccipital, which appears to be a small element lying dorso-laterally in a plane anterior to that of the condyle. A groove on the dorsal surface of the basioccipital leads into the *foramen magnum*. A notochordal pit lies in the centre of a shallow concavity in the postero-ventral surface of the condyle.

The supraoccipital (S.Oc.) appears to form the major part of the median portion of the occipital plate. Laterally it stretches to the inner base of the prominent ridge composed of the tabular, squamosal and paroccipital and forming the inner rampart of the auditory groove, and here it meets the tabular in a long vertical suture. In its ventro-lateral part the supraoccipital forms the upper border of the slit-like posttemporal fossa. Medially and laterally to the posttemporal fossa it meets the paroccipital and enters the upper edge of the jugular foramen. Dorsally its junction with the interparietal cannot be determined, but with this bone it forms the median occipital ridge to which it contributes the lower, narrower part.

The interparietal (I.P.) forms the dorso-median part of the occipit but it is uncertain how far it stretches ventrally before meeting the supraoccipital. It forms the dorsal part of the median ridge, which, in *whaitsi*, is broad in its interparietal part but in *akraalensis* is sharp and narrow throughout.

The tabular (Tab.) as I have determined its limits, forms only a small part of the occipital surface as it appears not to stretch far medially. It forms the greater part of the prominent lateral ridge lying medially to the auditory groove. Dorsally the tabular flanks the postero-lateral parietal flange and the upsweeping dorsal squamosal flange and thus forms the postero-dorsal part of the temporal arch. This part of the tabular is especially strong in *akraalensis*, and here its dorsal edge is wide, strong and rugose.

The paroccipital (P.Oc.) in occipital view is seen to be a strong bar medially abutting against the basioccipital and stretching laterally to the lateral ridge

where its dorso-lateral corner forms the most prominent part of this ridge. Its ventro-lateral edge overlaps and supports the quadrate and dorsally it meets the supraoccipital and forms the lower border of the small slit-like posttemporal fossa and that of the small *foramen jugale*. Medially to the jugular foramen it meets the ventral edge of the exoccipital.

The quadrate (Q.) in occipital view shows a squarish posterior surface with, ventrally, paired strong rounded knobs separated by a broad groove together forming the ginglymoid articulatory surface for the articular. Laterally the quadrate is overlapped by the squamosal and flanked by the quadratojugal. Dorsally the posterior face of the quadrate is overlapped by the paroccipital. Medially the long quadrate ramus of the pterygoid is applied to its inner surface ventral to where the expanded distal end of the stapes abuts against the quadrate.

The quadratojugal (Q.J.) in posterior view is seen to form the latero-ventral corner of the skull. Dorsally its posterior surface is overlapped by the squamosal.

The stapes (St.) is only partly exposed in occipital view. It is a stout rod with its proximal end obscured by the paroccipital and its distal expanded end is seen to be applied to the inner face of the quadrate.

The pterygoid (Pt.) only shows its long quadrate ramus in occipital view. This is seen to extend very far posteriorly with its dorsal edge overlapping the distal end of the stapes and its postero-lateral end applied to the inner face of the quadrate.

If my interpretation of the relations of the interparietal, supraoccipital, tabular and paroccipital is correct the structure of the occiput in *Struthiocephalus* differs greatly from the condition in *Mormosaurus*, *Taurocephalus*, *Tapinocephalus* and *Moschops*. In these forms the tabular has a much greater occipital surface and the supraoccipital is a much smaller bone. In *Taurocephalus* and *Moschops* the tabular forms the whole of the dorsal border of the posttemporal fossa, but in *Tapinocephalus* the tabular, as in *Struthiocephalus*, is excluded from the posttemporal fossa.

The Ventral Surface of the Skull (fig. 4)

The palate and the *basis cranii* lie in the same plane, with the strong lateral pterygoidal rami extending ventral to this plane and the suspensorium lying still further ventrally. Striking is the very anterior position of the articulatory surfaces of the quadrates, which lie anterior to the posterior third of the skull. The suborbital fossae are small, the *choanae* large and oval and the interpterygoid vacuity is a narrow slit not extending between the prevomers.

The basioccipital (B.Oc.), in ventral view, is seen to carry a strong condyle pear-shaped in outline. Postero-ventrally the condyle is circularly excavated round the notochordal pit. Anteriorly to the condyle the basioccipital forms a squarish plate of bone directed antero-ventrally to meet the surface of the basisphenoid at an obtuse angle in a not very secure ankylosis. This surface carries a low median ridge flanked by shallow oval depressions and the anterior and lateral edges are rounded. Laterally the basioccipital is flanked by the

small exoccipital, whose limits are uncertain. Anterior to the jugular foramen the basioccipital is strongly supported by the paroccipital which it meets in a firm curved suture.

The basisphenoid (B.Sph.) posteriorly meets the basioccipital at an angle so that the two ventral surfaces subtend an obtuse angle. The postero-lateral corner of the basisphenoid forms the anterior border of the *foramen ovale*. Anteriorly the basisphenoid extends as a blunt wedge in between the pterygoids but the exact position of the suture is uncertain and its probable position is

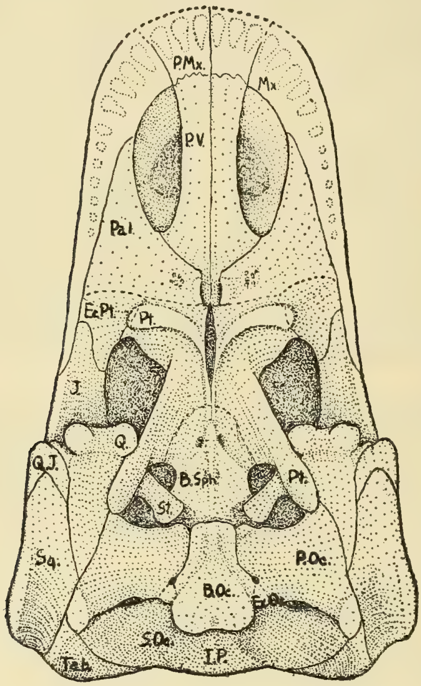


Fig. 4.—*Struthiocephalus whaitsi*. Ventral view of the skull (S.A.M. 11591) ($\times \frac{1}{6}$).

given in broken lines. In the median line the basisphenoid carries a low, sharp keel, lateral to whose anterior end lie the carotid foramina.

The pterygoids (Pt.) form a large part of the ventral surface. In the middle of the skull each pterygoid consists of a thin plate of bone meeting the basisphenoid obliquely along a long edge whose exact position has not been determined but which I believe stretches in anterior direction to the median line from the notch leading into the pituitary fossa. In the median line the pterygoid meets its fellow to form a sharp median keel. Anterior to this keel lies the interpterygoid slit. Lateral to the median keel the pterygoid is deeply excavated and lateral to this wide and deep groove lies the quadrate ramus of the pterygoid. This is a deep sheet of bone lying obliquely in the skull nearly at right

angles to the plane of the palate. The quadrate ramus extends far posteriorly and here its outer surface is applied to the inner face of the quadrate, well behind the plane of the condyle of the quadrate, and there is thus no anterior process of the quadrate to meet the pterygoid. The distal end of the stapes thus passes over the upper edge of the quadrate ramus of the pterygoid to reach the medial face of the quadrate. In no other Deinocephalian is the quadrate ramus of the pterygoid known to extend so far posterior to the quadrate condyle, which fact emphasizes how far the quadrate has shifted in an anterior direction.

The lateral ramus of the pterygoid is only moderately strong and has no great ventral extent. This is in strong contrast to the condition in the Titanosuchids where the ramus is very strongly developed. In *Struthiocephalus* the ramus does not extend far laterally as it does in *Taurocephalus* and all the Titanosuchids. The lateral edge of the ramus is supported by a descending process of the ectopterygoid, which, on account of the narrowness of the lateral pterygoid ramus, has a greater palatal face than in all other Deinocephalians. As in all Deinocephalians the lateral ramus is connected with the quadrate ramus by a web of bone reducing the size of the suborbital vacuity of which it forms the antero-median border. Anteriorly the exact limits of the pterygoid are indetermined but are probably as indicated by broken lines in the figures.

The ectopterygoid (Ec.Pt.) has a larger palatal surface than in other Deinocephalians. Its anterior and median limits are not clearly shown but it appears to descend along the lateral edge of the lateral pterygoid ramus which it buttresses. Its posterior edge forms the antero-lateral border of the suborbital fossa. Postero-laterally it abuts against the jugal in a sigmoid suture and laterally against the maxilla.

The palatine (Pal.), from where the suture with the pterygoid and ectopterygoid appears to lie, stretches antero-laterally as a thickened bone to form the rounded lateral two-thirds of the choanal border, and has its lateral edge applied to the inner maxillary surface where it flanks the alveolar border. Near the median line the palatine ends with a short sharp ridge running parallel to the median line. The two palatines thus do not meet each other, as median to their inner ridged borders a posterior tongue of the prevomers intervenes. Just lateral to the ridged inner edge there lies a rounded mound on which there are indications of the roots of a small number of small palatine teeth.

The prevomers (P.V.) are strong elements together forming a massive interchoanal bar. Anteriorly they underlie the inner surface of the premaxillaries with their anterior edges bevelled. Posteriorly they widen and overlie the palatines postero-laterally and in the median line send a tongue posteriorly in between the ridged inner edges of the palatines. Anteriorly the median suture is open and the interchoanal bar is here grooved, whereas in the posterior half of the bar a keel is developed along the median line.

The premaxillary (P.Mx.) alveolar border is very massive. Each premaxilla carries three strong teeth which are directed antero-ventrally. Posterior to the functional teeth there are indications of crowns which may be either replacing

or replaced teeth. In a juvenile specimen of *whaitsi* (S.A.M. 11493) where the crowns of the teeth are just erupting the labial edge of the premaxillaries is sharp and appears to form a cutting edge functioning as such until the teeth are sufficiently developed.

The maxilla (Mx.) has its alveolar border anteriorly massive and wide but then it tapers rapidly in posterior direction, and behind the last tooth a sharp edge is continued by the jugal, sweeping down towards the quadrato-jugal. Stumps of teeth and infilled alveoli in most specimens show that there were ten to eleven maxillary teeth. The anterior four are large, the fifth appreciably smaller, the sixth abruptly smaller and the series then decreases gradually in size in posterior direction. In the juvenile specimen of *whaitsi* (S.A.M. 11493) the labial edge of the maxilla, as is the case in the premaxilla, is sharp and during immaturity apparently forms a cutting edge.

The jugal (J) in ventral view has a narrow and deep flange of bone sweeping from the sharp outer edge of the maxilla down towards the quadratojugal. Internally and dorsally to this sharp edge the jugal is thickened and extending internally forms the lateral border of the suborbital fossa, and anteriorly it meets the ectopterygoid in a sigmoid suture.

The quadrate (Q) has its articulatory condyle very prominent in ventral view as this forms the most ventral part of the skull. The articulatory surface has a median trochlear surface bounded internally and externally by longitudinally oval condyles. The rounded articulatory surfaces are sharply demarcated from both the posterior and the anterior face of the upper part of the bone. Laterally a ridge bounded medially and laterally by a groove lies lateral to the condyle in the plane of the ventral edge of the quadratojugal. Dorsally the posterior surface of the quadrate is seen wedged in between the paroccipital internally and the quadratojugal and squamosal externally. Internally the long quadrate ramus of the pterygoid is applied to the medio-posterior face of the quadrate. The extremity of the ramus extends far posteriorly of the plane of the quadrate condyle and there is no anterior process of the quadrate to meet the quadrate ramus of the pterygoid. No *foramen quadrati* could be located with certainty but it may be small and may lie just medio-dorsally of the ridge on the quadrate lying laterally to the condyle.

The stapes (St.) is in position in S.A.M. 11591 on both sides. It is a stout rod with expanded distal and proximal ends. The distal end applied to the inner face of the quadrate is underlain by the long quadrate ramus of the pterygoid and has its postero-distal corner much expanded. No foramen can be determined.

The quadratojugal (Q.J.) in ventral view is seen to form the angle of the 'cheek'. Its ventral edge lies in a plane dorsal to the condyle of the quadrate from which it is separated by a ridge bounded on both sides by a groove. The posterior surface of the quadratojugal is seen to be overlapped by the descending posterior squamosal process.

The squamosal (Sq.) in ventral view forms the outer edge of the posterior third of the skull. Median to this edge lies the auditory groove whose inner wall is formed by a ridge formed by the squamosal, paroccipital and tabular. Further ventrally the squamosal supports the posterior face of the quadratojugal and quadrate.

The paroccipital (P.Oc.) shows a much greater face in ventral view than it does in occipital view. This rotation of the paroccipital from the occipital plane on to the ventral surface is one of the results of the forward shift of the quadrates and is a character distinguishing all Deinocephalians from the other Therapsids.

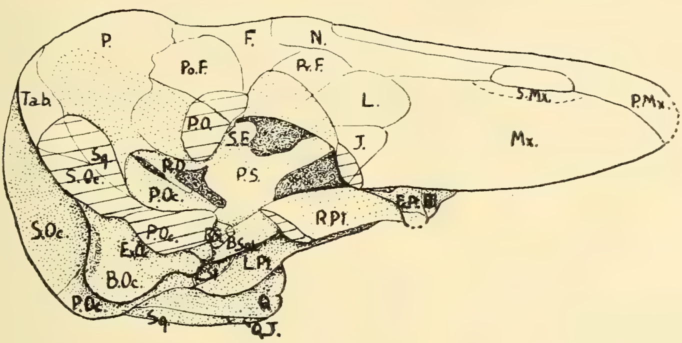


FIG. 5.—*Struthiocephalus whaitsi.* The right side of the braincase in lateral view (S.A.M. 11591) ($\times \frac{1}{8}$). The suborbital bar, postorbital bar and occipital plate fractured and here seen in section. The right quadrate ramus of the pterygoid and the right stapes are also seen in section where they have been fractured.

The paroccipital is a strong massive element acting as a very firm connecting link between the bones of the 'cheek' and the suspensorium lying laterally and the basioccipital of the cranial base. Posteriorly the thickening of the paroccipital and supraoccipital have all but obliterated the posttemporal fossa which is only preserved as a narrow slit. The postero-lateral corner of the paroccipital forms the most prominent part of the strong ridge from which the depressor mandibulae originates. Antero-medially the paroccipital forms the posterior half of the border of the *foramen ovale*.

In ventral view the tabulars, interparietal and supraoccipitals are seen to lie well posterior to the basioccipital condyle with the first two forming the posterior edge of the skull which, as is the case in most Tapinocephalids, is nearly a straight line, whereas in the Titanosuchids this edge is concave. In *akraalensis* more of the occiput is seen in ventral view than is the case in *whaitsi*.

The Braincase in Lateral View (fig. 5)

In a specimen of *whaitsi* (S.A.M. 11591) a fracture through the posttemporal arch, postorbital and suborbital bars has enabled me to prepare the lateral surface of the braincase on the right side. But after the removal of the intractable

matrix from the temporal fossa and orbit the surface of the internal bones thus exposed is not sufficiently clear so as to determine the limits of the constituent bones with any great degree of certainty. The accompanying figure shows what structural details have been determined. The parasphenoid (P.S.) is the largest element forming a large part of the fenestrated septum. A dorsal sheet of bone supports the ventral edge of the sphenethmoid and a well-developed anterior process is directed obliquely forwards. Of this part of the parasphenoid Efremof says that in many cases, 'den vordere Forsatz des Parasphenoid knorpelig blieb', whereas in fact the parasphenoid is an *os investitiens* and thus not an element preformed in cartilage.

Of the sphenethmoid (S.E.) only the lower part can be seen where it rests on the upper edge of the dorsal parasphenoidal process.

The prootic (P.O.) is seen wedged in the postero-dorsal corner and its relations with the sphenethmoid are uncertain.

The opening for the trigeminus and the fenestra of the fossa hypophyseos are situated as shown in the figure.

The Lower Jaw

In S.A.M. 11693 most of the dentaries are preserved and in S.A.M. 11493 the crushed posterior half of the right mandibulary ramus is present, but in both only the outer surface could be prepared. What could be determined of the structure I have included in the composite figure accompanying the description of *Struthiocephaloides duplessisi*.

The hinge of the lower jaw lies very far forward, in the plane of the orbit. The dentary forms nearly two-thirds of the ramus and its mentum is massive and fairly upright. The teeth are directed upwards and only slightly outwards to intermesh with the labially directed teeth of the upper jaw. The angular has a large outer flange and the surangular has a strong rounded dorsal border curving upwards and forwards from the articular.

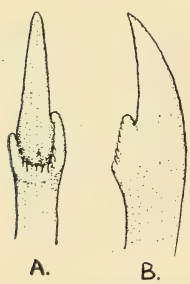


Fig. 6.—*Struthiocephalus whaitsi*. A tooth of the lower jaw (S.A.M. 11591) ($\times \frac{1}{2}$). *a*, lingual view. *b*, lateral view.

The Dentition (fig. 6)

In all specimens stumps, imperfect crowns and empty alveoli are all that are preserved. In fragments of the lower jaw of S.A.M. 11591 a few crowns of the teeth of the lower jaw are preserved and one is figured here.

All the teeth have a labial talon or pointed cusp at whose base there lies lingually a cup-shaped base with a serrated edge.

The three teeth in the premaxilla and the first four maxillary teeth are large with long labial cusps. Then abruptly the fifth tooth is much smaller with a short labial talon and then the rest of the teeth decrease still further in size posteriorly.

A tooth just erupting in the lower jaw (S.A.M. 11591), which is thus as yet unabraded, shows three longitudinal ridges on the lingual surface of the talon. With use the talon is abraded and the ridges disappear. Through use the serrations on the labial edge of the cup are also worn down and lost.

There are indications that in the anterior teeth there can be at least three successive sets of teeth.

Taxonomic Diagnoses

As Mormosaurids I have grouped together (1936) the genera *Mormosaurus*, *Struthiocephalus* and *Taurocephalus*. The following amended diagnosis for this group is suggested: Skull large, long and moderately wide; snout long or fairly long and shallow; cranial bones strongly thickened with parietal, naso-frontal and postorbital bosses undeveloped, distinctly developed or tending to coalesce in the general pachyostosis; postorbital bar moderately wide to wide and massive; the facial surface fairly or very abruptly demarcated from the thickened cranial surface; temporal fossae fairly small with the dorso-ventral diameter appreciably or not very much greater than the antero-posterior; intertemporal region fairly narrow to moderately wide and laterally distinctly or only slightly bayed; parietals entering supratemporal border; quadrate ramus of the pterygoid extending only up to or well posterior to the quadratic condyle, which is situated far forward; tabular entering or not entering the post-temporal fossa; no differentiation of teeth into incisors, canines and postcanines.

Generic Diagnoses

A. *Mormosaurus*

1. Snout short, very shallow, facial surface not extending posterior to the anterior orbital border, very abrupt transition from the facial to the cranial surface.
2. Dorsal cranial surface very strongly pachyostosed, with the centres of thickening coalesced and transition on to face very abrupt along a very definite transverse line forming a transverse wall.
3. Additional pachyostosis:
   - *a.* Nasal boss laterally confluent with the thickening of the postorbital bar and the prefrontal and thus forming a transverse wall from orbit to orbit.
   - *b.* Parietal boss not very distinct, confluent with the general pachyostosis of the parietal and frontal.
   - *c.* Postorbital bar wide and massive but without distinct bulbous boss and thus flowing evenly on to the general dorsally thickened surface.
   - *d.* Posttemporal arch greatly thickened and rugose.
   - *e.* Orbits not visible in dorsal view and in dorsal view the postorbitals do not form the lateral border of the skull.
   - *f.* Antero-posterior diameter of temporal fossa small and fossa transversely oval.
   - *g.* Dorsal parietal surface fairly wide, laterally indistinctly bayed.

4. Dentition feeble, uniform.
5. Quadrate moderately far forward with the quadrate ramus of the pterygoid not extending much posterior to the plane of the quadratic condyle, not underlying the distal end of the stapes.
6. The lateral ramus of the pterygoid does not form a prominent transverse bar and the width across the transverse rami is small.
7. The intersquamosal width is large.
8. The basioccipital condyle is directed posteriorly.
9. The frontal appears to be small and is excluded from the orbital border, the supraoccipital is wide and low, the tabular with a moderate occipital face and apparently enters the posttemporal fossa, the lacrimal meets the nasal, the squamosal with an anterior wedge into the jugal. (This diagnosis is based on Watson's description and figures.)

B. *Struthiocephalus*

1. Snout long, shallow, facial surface extending far back, posterior to the anterior orbital border, fairly abrupt transition on to the cranial surface.
2. Dorsal cranial surface strongly pachyostosed, but centres of greatest thickening still distinct and the transition on to the face fairly abrupt but not along a definite line and thus not forming a transverse wall.
3. Additional pachyostosis:
   - *a.* Naso-frontal boss not laterally confluent with the pachyostosis of the postorbital bar and the prefrontal and thus not forming a transverse wall from orbit to orbit.
   - *b.* Parietal boss distinct.
   - *c.* Postorbital bar moderately wide to wide, fairly massive to massive, with or without distinct bulbous boss and with or without a ridge demarcating it from the dorsal surface.
   - *d.* Posttemporal arch moderately to greatly thickened, fairly smooth to rugose.
   - *e.* Orbits just visible in dorsal view, and in dorsal view the postorbitals do not form the lateral border of the skull.
   - *f.* Antero-posterior diameter of temporal fossa moderate to fairly small and fossa oval to slitlike.
   - *g.* Dorsal parietal surface narrow to moderately wide, laterally distinctly or indistinctly bayed.
4. Dentition well developed with 14 teeth of which 3 are on the premaxilla; the fifth maxillary tooth is abruptly smaller than those anterior to it and then posteriorly the series gradually decreases in size.
5. Quadrate far forward with the quadrate ramus of the pterygoid extending much posterior to the plane of the quadratic condyles, underlying the distal end of the stapes.
6. The lateral ramus of the pterygoid forms a strong and prominent bar but the width across the transverse rami is small.

7. The intersquamosal width is moderate to fairly moderate.
8. The basioccipital condyle is directed postero-ventrally.
9. The frontal is of medium size and enters the orbital border, the supraoccipital is wide but apparently fairly high, the tabular with a small occipital face and excluded from the posttemporal fossa, the lacrimal meets or does not meet the nasal, the squamosal without anterior wedge into the jugal.

C. *Taurocephalus*

1. Snout of medium length, fairly high, facial surface not extending posterior to the anterior orbital border, transition on to cranial surface not abrupt but through a gentle curve.
2. Dorsal cranial surface fairly strongly pachyostosed, but centres of greatest thickening still distinct and the transition on to the face through a gentle curve and no transverse wall is thus formed.
3. Additional pachyostosis:
   a. No distinct naso-frontal boss present, and from orbit to orbit the dorsal surface is evenly convex.
   b. The parietal boss forms a rounded mound, highest round the pineal border but with its edges running into the general parietal surface.
   c. Postorbital bar fairly wide and massive, though extending very far laterally it is dorsally not bulbous and flows evenly on to the generally thickened dorsal surface; the width over the postorbitals is very great and in dorsal view they form the lateral edge of the skull.
   d. Posttemporal arch moderately thick and smooth.
   e. Orbits just visible in dorsal view anterior to the postorbital bar which here forms the lateral border of the skull in dorsal view.
   f. Antero-posterior diameter of the temporal fossa fairly great and thus broadly oval.
   g. Dorsal parietal surface wide and laterally distinctly bayed.
4. Dentition well developed with 21 teeth of which 4 are in the premaxilla; there is an evenly graded decrease in size in posterior direction.
5. Quadrate not very far forward; the quadrate ramus of the pterygoid not extending posterior to the plane of the quadratic condyles, only underlying the anterior corner of the distal end of the stapes; quadrate with anterior process meeting the quadrate ramus of the pterygoid.
6. The lateral ramus of the pterygoid forms a strong and prominent bar and the width across the transverse rami is large.
7. The intersquamosal width is moderate, just more than the inter-postorbital width.
8. The basioccipital condyle is directed posteriorly.
9. The frontal is large and enters the orbital border, the supraoccipital is narrow and high, the tabular has a large occipital face and enters the posttemporal fossa, the lacrimal does not meet the nasal, the squamosal with a sharp anterior wedge into the jugal.

D. *Struthiocephaloides*[9]

1. Snout long, shallow, facial surface extending far back, posterior to the anterior orbital border, transition on to the cranial surface not abrupt.
2. Dorsal cranial surface strongly pachyostosed, but centres of greatest thickening still fairly distinct, but the transition on to the face not abrupt, with no indication of a transverse interorbital step.
3. Additional pachyostosis:
   a. No naso-frontal boss (but with a swelling just anterior to the posterior end of the premaxilla in *cavifrons*).
   b. Parietal boss distinct in *cavifrons* but in *duplessisi* undeveloped or indistinct due to confluence with the general pachyostosis of the parietal and frontal.
   c. Postorbital bar very wide, massive, but without a bulbous boss in its dorsal part.
   d. Posttemporal arch moderately to strongly thickened, fairly smooth.
   e. Orbits just to plainly visible in dorsal view, and in dorsal view the postorbitals do not form the lateral border of the skull.
   f. Antero-posterior diameter of temporal fossa moderate to fairly large, fossa oval or narrow (in *cavifrons* the fossa lies obliquely in the skull).
   g. Dorsal, parietal surface wide, laterally not pinched in.
4. Dentition well developed with 14 teeth of which 3 are in the premaxilla, and from the 5th the teeth gradually decrease in size.
5. Quadrate far forward, with the quadrate ramus of the pterygoid extending much posterior to the plane of the quadratic condyles.
6. The lateral ramus of the pterygoid forms a fairly strong and prominent bar but the width across the transverse rami is small.
7. The intersquamosal width is moderate to large.
8. The basioccipital condyle is directed much ventrally.
9. The frontal is fairly small, entering the orbital border in *duplessisi* but not in *cavifrons*, the tabular excluded from the temporal fossa, the lacrimal does not meet the nasal, the squamosal without anterior wedge in to the jugal.

E. *Struthionops*[10]

1. Snout fairly short and high, facial surface not extending posterior to anterior orbital border, transition to cranial surface not abrupt but through a gentle curve.
2. Dorsal cranial surface moderately pachyostosed, centres of greatest thickening distinct, no interorbital step.
3. Additional pachyostosis:
   a. Naso-frontal boss very low and not confluent with the thickening on the prefrontals.
   b. The parietal boss is a fairly prominent mound, highest round the pineal foramen and with its outer edges running into the general parietal surface.

Reconstruction of STRUTHIOCEPHALUS

Photograph of the head of *Struthiocephalus* taken from the life-sized reconstruction in plaster of the whole animal as exhibited in the South African Museum. Modelled by the author.

c. Postorbital bar fairly narrow and slender with dorsal swelling.
d. Posttemporal arch fairly weak and smooth.
e. Orbits large and well visible in dorsal view, postorbitals form the lateral border of the skull as seen in dorsal view.
f. Antero-posterior diameter of temporal fossa fairly large and broadly oval.
g. Dorsal parietal surface wide, but laterally slightly, pinched in.

4. Dentition with probably 14–15 teeth evenly decreasing in size in posterior direction.
5. Quadrate not far forward.
6. The lateral ramus of the pterygoid strong and prominent but transverse width across the rami moderate.
7. The intersquamosal width is large, just more than the inter-postorbital width.
8. The basioccipital condyle is not preserved.
9. The frontal is large, but is just excluded from the orbital border, the lacrimal just meets the nasal, the squamosal without a wedge into the jugal.

Diagnoses for the Species of Struthiocephalus

S. whaitsi

1. Naso-frontal, parietal and bulbous boss on postorbital prominent.
2. Snout moderately long, shallow and fairly weak.
3. Moderately broad over squamosals.
4. Pineal foramen moderately far from occipital border.
5. Postorbital bar wide.
6. Temporal fossa fairly rounded.
7. Median occipital ridge wedge-shaped with rounded edges.
8. Nares well back.
9. Quadrate well forward.
10. Interorbital width large.
11. Interparietal width small.
12. Posttemporal arch moderately strong.

S. rheederi

1. Naso-frontal, parietal and bulbous boss on postorbital prominent.
2. Snout fairly long, moderately shallow but broad.
3. Broad over squamosals.
4. Pineal foramen very near occipital border.
5. Postorbital bar probably wide (not evident from Broom's account).
6. Temporal fossa slit-like.
7. Median occipital ridge not figured or described by Broom.
8. Nares very far back.
9. Quadrate not figured or described by Broom.
10. Interorbital width very large.
11. Interparietal width large.
12. Posttemporal arch moderately strong.

S. milleri

1. Naso-frontal and parietal bosses very prominent and bulbous boss on postorbital bar moderately prominent.
2. Snout very long and very shallow.
3. Relatively narrow over squamosals.
4. Pineal foramen near occipital border.
5. Postorbital bar narrow.
6. Temporal fossa fairly rounded.
7. Median occipital ridge not figured or described by Olson and Broom.
8. Nares fairly near premaxillary edge.
9. Quadrate not figured or described by Olson and Broom.

10. Interorbital width small.
11. Interparietal width fairly small.
12. Posttemporal arch robust.

S. akraalensis

1. Naso-frontal boss large but low, parietal boss prominent, postorbital bar dorsally greatly thickened with the development of a longitudinal ridge raised above the surface of the frontal which thus appears excavated.
2. Snout very long and shallow.
3. Broad over the squamosals.
4. Pineal foramen far from occipital border.
5. Postorbital bar very wide and strongly rugose.
6. Temporal fossa slit-like.
7. Median occipital ridge straight with sharp median edge.
8. Nares far back.
9. Quadrates very far forward.
10. Interorbital width very large.
11. Interparietal width very large.
12. Posttemporal arch very robust.

The Chief Measurements Compared

	whaitsi	*rheederi*	*milleri*	*akraalensis*
Length	558	624	480	655
Width	345	432	300	390
Interorbital width	170	180	130	175
Interparietal width	100	140	115	167
Pineal foramen to occipital edge	65	48	44	90
Naris to Pr. Mx. edge	85	114	52	95

Keys to Facilitate Rapid Taxonomic Identification

Deinocephalia. Large therapsids, with pachyostosed skulls, with large quadrates, quadratojugals forming the corner of the 'cheek', premaxillaries with long facial exposure.

Titanosuchia. Deinocephalians with differentiated carnivorous dentition, cranial bones not greatly pachyostosed, snout long, low parietal crest, quadrates not situated far anteriorly.

Tapinocephalia. Medium-sized to large Deinocephalians with undifferentiated herbivorous dentition, cranial bones slightly to very greatly pachyostosed, in all but the Moschosaurids the snout is weakened, there is no parietal crest (except in *Riebeeckosaurus* and *Avenantia*); the quadrates are situated moderately to very far anteriorly.

Groups in the Tapinocephalia

1. Little pachyostosis . . . *Moschosaurus*-group
2. Great pachyostosis . . . 3
3. Facial bones thickened to run evenly on to the cranial surface . . . *Moschops*-group
4. Facial bones not so thickened as to run evenly on to the cranial surface . . . 5
5. Snout very much shortened and weakened . . . *Tapinocephalus*-group
6. Snout not very much shortened and weakened . . . *Mormosaurus*-group

Genera of the Mormosaurus-group

1. Skull with abrupt step from face to cranial surface . . *Mormosaurus*
2. Skull without abrupt step . . . 3
3. Distinct naso-frontal boss present . . . *Struthiocephalus*
4. Distinct naso-frontal boss absent . . . 5
5. Width over postorbitals not very great and postorbitals not forming lateral edge of skull in dorsal view . . . *Struthiocephaloides*
6. Width over parietals great and postorbitals forming lateral edge of skull in dorsal view . . . 7
7. Width across jugals much less than across postorbitals . *Taurocephalus*
8. Width across jugals not much less than across postorbitals *Struthionops*

THE SPECIES OF STRUTHIOCEPHALUS

1.	Snout very long and very shallow	*milleri*
2.	Snout not very long and very shallow	3
3.	With prominent ridge median to postorbital boss . . .	*akraalensis*
4.	Without this ridge	5
5.	Pineal foramen very near occipital border	*rheederi*
6.	Pineal foramen not near occipital border	*whaitsi*

DISCUSSION

It would be unwise to attempt a discussion of the relationships of the Deinocephalians with other orders and *inter se* until all the material in the South African Museum has been studied. At this stage I am confining my remarks to some points which the study of *Struthiocephalus* has brought to the fore.

Age in the Struthiocephalus skull

A specimen of *whaitsi* (S.A.M. 11493) has a skull just as long as that of the type (S.A.M. 2678) and another specimen referred to this species (S.A.M. 11591), but in it the upper teeth are just commencing to erupt and the outer edge of both premaxillaries and maxillaries is sharp and appears to form a functioning cutting edge until the teeth are fully erupted. All the cranial bones are still little affected by any pachyostosis. The postorbital bar is narrow and lightly built with only its dorsal part slightly expanded and here the postfrontal is large and has not yet overgrown the postorbital. The posterior flange of the postorbital forming the dorsal border of the temporal fossa is little reduced and though not meeting the squamosal extends far posteriorly and is not encroached on or overhung by the parietal. The antero-posterior diameter of the temporal fossa is nearly equal to the dorso-ventral diameter. The posttemporal arch is not thickened and does not encroach into the fossa. The quadrates still lie in a plane posterior to the anterior orbital border. The whole outer surface is still smooth and free from rugosities. Unfortunately the state of preservation does not reveal the structure of the occiput and the ventral aspect of the skull. What could be determined in this juvenile skull is however sufficient to show that many of the characters peculiar to the adult Tapinocephalian skull are mainly due to the pachyostosis which increasing age brings about and which obscures its essential therapsid nature.

The Cranial Pachyostosis

Apart from the fact that in both *Moschops* and *Struthiocephalus* an intensification of the thickening of the cranial bones takes place during the life of the individual, it also appears to be a process that can be traced phyletically.

In *Moschosaurus*, which is undoubtedly the most primitive of the South African Tapinocephalians, there is very little pachyostosis and in *Agnosaurus* it is also slight, whereas in all the other known forms a lesser or greater degree of bone-thickening is apparent. Less of the skull is affected in the *Mormosaurus*-group than in the *Moschops*- and *Tapinocephalus*-groups. The thickening chiefly affects the supra- and interorbital region, the intertemporal skull roof, the post-orbital bar; the posttemporal arch and the face and 'cheek' are relatively little

affected. The thickening in these regions very materially affects the size and shape of the temporal fossa, the orbits, the braincase and the mechanism of the lower jaw.

The Supra- and Interorbital region

In the *Mormosaurus*-group the moderate to fairly strong pachyostosis lies posterior to the plane of the anterior orbital border. It is least in *Struthiocephalus*, *Struthiocephaloides*, and *Struthionops*, and here the relatively unaffected snout extends posteriorly to the plane of the anterior orbital border where the transition on to the supraorbital thickened part is not very abrupt. This transition is not very abrupt chiefly because the pachyostosis has not affected the lacrimal, prefrontal, nasal and frontal to any great extent, only the posterior part of the prefrontal and nasal and the medio-anterior part of the frontal being affected. The thickening here does not extend transversely across the skull from orbit to orbit, but is in evidence at three separate centres, viz. the tops of the two postorbital bars and in the naso-frontal boss. In *Taurocephalus* more of the prefrontal and the posterior part of the nasals are affected and the above-mentioned three centres tend to coalesce and the transition from the face on to the cranium is by a gentle curve. In *Mormosaurus* the process has extended further and the pachyostosis extends anterior to the plane of the anterior orbital border with confluence of the three centres to form a very distinct transverse step raised high above the surface of the snout.

In the *Tapinocephalus*-group this process has progressed much further in *Tapinocephalus* to include all the prefrontal, frontal and the posterior part of the nasal to a plane well in advance of the anterior orbital border and the descent on to the surface of the snout is very abrupt from the very high transverse rampart. (But in *Keratocephalus* this region has remained essentially *Struthiocephalus*-like with an accentuation of the naso-frontal boss.)

In the *Moschops*-group the pachyostosis is continued into the bones of the snout but is so graded that instead of forming a step there is an even curve from the tip of the snout on to the supra- and interorbital region.

The Intertemporal Skull Roof

In *Moschosaurus* and *Agnosaurus* the intertemporal width is small with the sides pinched in and with little thickening of the parietal. In the *Mormosaurus*-group this width is increased with the stages in this process shown by the five genera *Struthiocephalus*, *Struthiocephaloides*, *Struthionops*, *Taurocephalus* and *Mormosaurus*, in this order. In *Struthiocephalus* this widening has advanced least but the direction of this process is evident in the series formed by its constituent species. The loss of the dorsal bay to the temporal fossa can be traced through the species of *Struthiocephalus* to *Mormosaurus*.

In the *Tapinocephalus*-group the intertemporal width attains its greatest dimensions and there is no sign of the bay.

In *Moschops* a parallel process of widening of the intertemporal region has taken place but there is still evidence of the bay.

The thickening of the parietal is at first mainly in evidence round the pineal foramen. In *Struthiocephalus* the thickness of the parietal at the pineal foramen varies from 40 to 80 mm. and in a Tapinocephalid species from Gunyanka's Kraal in Southern Rhodesia it reaches the enormous thickness of 310 mm. With the increasing pachyostosis of the parietal the boss round the pineal foramen tends to become engulfed by the general thickening and in the Rhodesian specimen there is little evidence of a separate pineal boss.

The Postorbital Bar

The postorbital bar is light and slender in *Moschosaurus* and *Agnosaurus*, moderate in *Taurocephalus* and *Struthionops*, strong to very strong in *Struthiocephalus* and *Struthiocephaloides*, very strong and massive in *Mormosaurus*, and very wide, strong and very massive in *Tapinocephalus*. In *Struthiocephalus* the dorsal end of the bar formed by the postfrontal has a tendency to form a bulbous boss reminiscent of the condition in the Titanosuchid *Anteosaurus*, but in *Tapinocephalus* especially this is incorporated in the general extensive pachyostosis. An increasing massiveness of the posttemporal arch parallels that of the postorbital bar, and together they have the effect of reducing the antero-posterior diameter of the temporal fossa.

Adverse Effects of the Pachyostosis

The downward growth of the roof-bones, together with the reduction of the angle between skull roof and occiput, boxes in the braincase in the dorso-posterior corner of the skull. The encroachment of the posttemporal arch and postorbital bar very greatly reduces the size of the temporal fossa and consequently of the adductor mandibulae. The thickened bone overhanging the orbits very materially restricts the field of vision. No doubt the increasing pachyostosis indicates the road which led to extinction.

REFERENCES

[1a] Watson, D. M. S. *P.Z.S.*, p. 749. 1914.
[1b] Haughton, S. H. *Ann. S. Afr. Mus.*, xii, 2, p. 52. 1915.
[1c] Gregory, W. K. *Bull. Am. Mus. Nat. Hist.*, 61, p. 179. 1926.
[1d] Broom, R. *Mammal-like Reptiles of South Africa*, p. 18. 1932.
[1e] Boonstra, L. D. *Bull. Am. Mus. Nat. Hist.*, 72, p. 75. 1936.
[1f] Efremov, J. A. *Nova Acta Leopoldina*, N.F. 9, 39, p. 155. 1940.
[2] Boonstra, L. D. *Ann. Mag. Nat. Hist.*, xii, 5, p. 455. 1952.
[3] Boonstra, L. D. ibid., p. 509. 1952.
[4] Boonstra, L. D. *S. Afr. Jour. Sci.*, 48, 8, p. 247. 1952.
[5] Broom, R. *P.Z.S.*, p. 302. 1937.
[6] Olson, E. C., and Broom, R. *Journ. Pal.*, 4, 7, p. 615. 1937.
[7] Haughton, S. H. *Report of the South African Museum for* 1915, p. 4. 1916.
[8] Boonstra, L. D. *Tydskr. Wet. Kuns*, xii, 2, p. 237. 1952.
[9] Boonstra, L. D. ibid. xii, 2, p. 246.
[10] Boonstra, L. D. *Ann. Mag. Nat. Hist.* xii, 5, p. 988. 1952.
[11] Boonstra, L. D. *Tydskr. Wet. Kuns.* xii, 2, p. 242. 1952.

6. *The Lower Jaw Articulatory Region in some Pristerognathid Therocephalians.* By LIEUWE D. BOONSTRA, D.SC.

(With 4 text-figures)

In the course of the preparation of a paper, mainly of a taxonomic nature, for the *Annals of the South African Museum* on the hundred-odd specimens of Therocephalians from the *Tapinocephalus*-zone preserved in the South African Museum, I have determined certain points in the structure of the posterior part of the lower jaw and the relations of the quadrate, quadratojugal and squamosal.

A short account of the structure in some of the better-preserved specimens is presented here. New genera and species mentioned here will be fully described in the forthcoming taxonomic paper referred to above.

SCYMNOSAURUS FEROX (fig. 1)

A specimen collected by me on the farm Rietkuil in the district of Beaufort West (S.A.M. 9084) consists of a fairly good skull and parts of some limb-bones. By direct comparison with the type in our collection I have identified it with *Scymnosaurus ferox*. Natural weathering has partly exposed the mandibular articulatory region, but also unfortunately removed the lateral surface of the quadrate, quadratojugal and the lateral edge of the squamosal.

The dentary has a concave posterior edge overlapping the angular and its dorso-posterior coronoid process does not extend above the subtemporal arch but is directed more posteriorly in the direction of the squamosal.

The angular has a fairly large lateral face with a prominent dorso-ventral ridge and a lesser ridge roughly at right angles. The anterior half of its ventral edge is fairly thick, but the posterior half has a double thin edge—the outer being the reflected flange. Posteriorly the outer (reflected) flange extends to the surangular and ventrally it underlaps the articular. Dorsally there is a small notch, anterior to which the angular apparently overlapped the outer surangular face. This dorsal notch, not exposing the outer surface of the inner angular sheet, but instead the external surangular surface, thus has different relations than in other Pristerognathids where this region has been described. A notch in the ventral edge indicates the level to which the reflected flange usually extends posteriorly in other Pristerognathids.

Externally the surangular shows a thickened rounded and curved dorsal and postero-dorsal girder forming the edge of the mandible. Further ventrally the surangular curves firmly round the lateral surface of the articular and, with the internal prearticular, transmits the stresses arising anteriorly to the articular bone.

The articular is a comparatively small bone of peculiar shape; externally a tongue extending dorsally is anteriorly clasped by the surangular and posteriorly

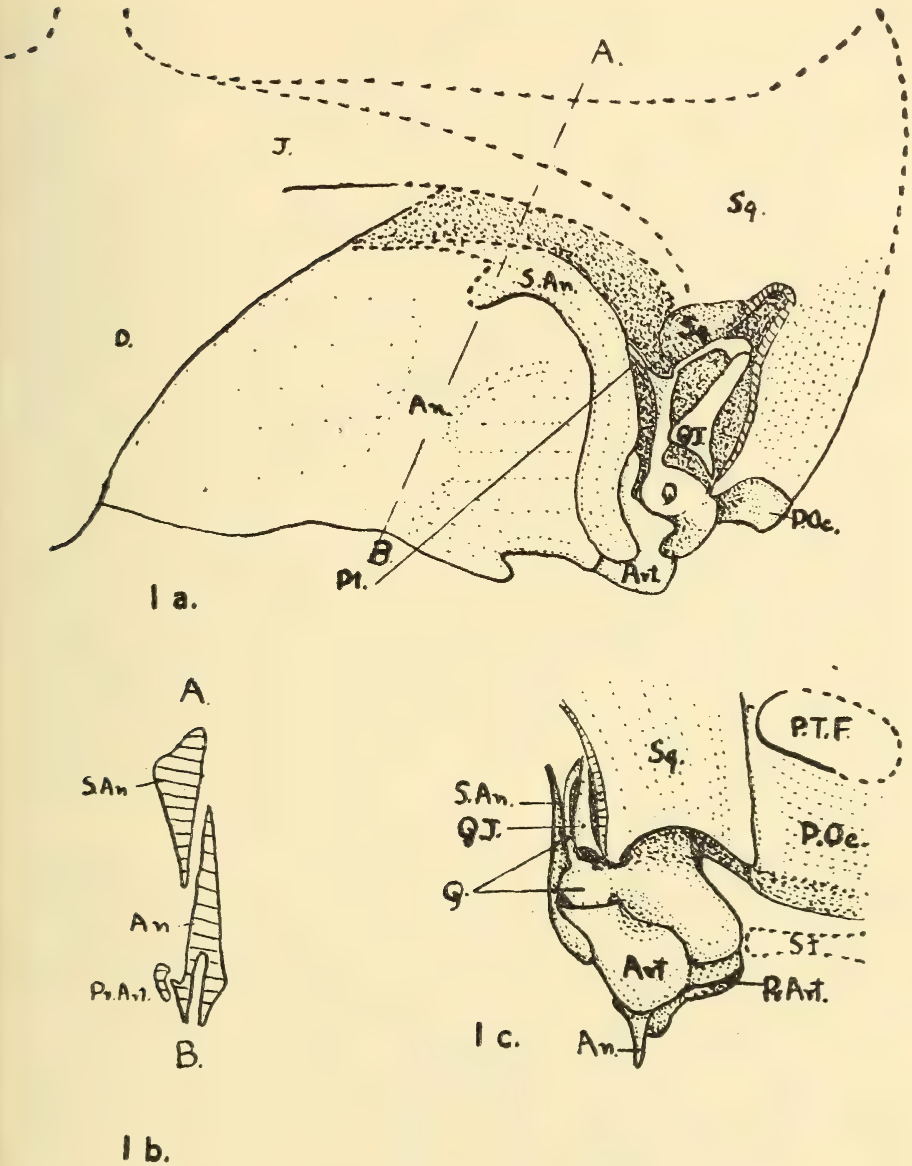


FIG. I.—*Scymnosaurus ferox.* S.A.M. 9084, Rietkuil, Beaufort West. (× ⅗ nat. size.)

a. Lateral view. The lateral surface of the quadrate, quadratojugal and squamosal has been weathered away so that these elements are seen in section.

b. Cross-section of above at A.B.

c. Oblique postero-lateral view. The lateral edge of the squamosal, quadrate and quadratojugal weathered and seen in section.

These and subsequent figures are all ortho-projections taken with a pantograph.

An.—angular. Art.—articular. B.Oc.—basioccipital. B.Sph.—basisphenoid. Cor.—coronoid. D.—dentary. Ep.Pt.—epipterygoid. Ex.Oc.—exoccipital. F.J.—foramen jugale. I.P.—interparietal. J.—jugal. Pa.—parietal. P.O.—postorbital. P.Oc.—paroccipital. Pr.Art.—prearticular. Pr.Ot.—proötic. P.T.F.—posttemporal fenestra. Pt.—pterygoid. Q.—quadrate. Q.J.—quadratojugal. S.A.(n)—surangular. S.Oc.—supra-occipital. Sq.—squamosal. St.—stapes. Tab.—tabular.

forms the front face for the articulation with the quadrate condyle; it then extends posteriorly to form the ventral part of the articulatory surface, but no retro-articular process is developed. In posterior view it is seen that the articular has a dorsal spur, which, if it extends anteriorly, must form a ridge dividing the articulatory surface into a smaller lateral concavity and a larger median concavity. The quadratic condyle would thus be bipartite with a smaller rounded outer and an inner larger roller-shaped condyle. Medio-ventrally the under-surface of the articular is clasped by the prearticular, which transmits the greater part of the thrust from the anterior part of the mandible to the articular.

Only part of the quadrate is exposed in lateral and in posterior view. Its lateral surface has been somewhat weathered away so that the drawing (fig. 1*a*) really shows a section face. The apparent bipartite nature of the quadratic condyle has been noted above. In section the outer condyle has a circular outline. From the antero-dorsal corner of this condyle the lateral edge of the quadrate is seen extending dorsally to meet the squamosal. Further medially a flange of the squamosal clasps the quadrate from above. From the antero-median corner of the quadrate a process stretches antero-medially to meet the quadrate ramus of the pterygoid. In posterior view it is seen that from the external condyle the quadrate extends medially, forming a transverse mass forming the major part of the articulatory surface. Dorsal to this transverse body the quadrate extends dorsally as a strong pillar of which the posterior surface is overlapped by a descending sheet of the squamosal. The medial face of the quadrate abuts against the latero-anterior corner of the strong paroccipital.

On the median surface of the internal condyle there appears to be a shallow depression for the reception of the distal end of the stapes. The tympanic membrane must have been situated in this region, but except for the ventral squamosal edge no other points of attachment can be determined.

The quadratojugal is only seen in section, where it is seen as a triangular element with its base resting on the postero-dorsal surface of the rounded external condyle and its apical part lying posterior to the ascending column of the quadrate and in the hollow between this and the descending flange of the squamosal. The median limits of the quadratojugal and the quadrate foramen are in posterior view hidden by the descending flange of the squamosal.

The squamosal has its lower antero-lateral edge weathered away and a section medial to this is shown in the figure. There is thus exposed much of the quadratojugal, the upper part of the quadrate and the internal forwardly directed domed sheet of the squamosal. All of which would be covered laterally by the squamosal when fully present. In posterior view the descending sheet of the squamosal covers the quadratojugal and most of the quadrate above the condyles. Its ventral edge is concave and probably served as an edge of attachment for the tympanic membrane. The median edge of the descending sheet of the squamosal forms a backwardly directed ridge where it abuts against the paroccipital. This ridge forms the median wall of the auditory groove, which is thus situated directly dorsal of the probable location of the tympanic membrane.

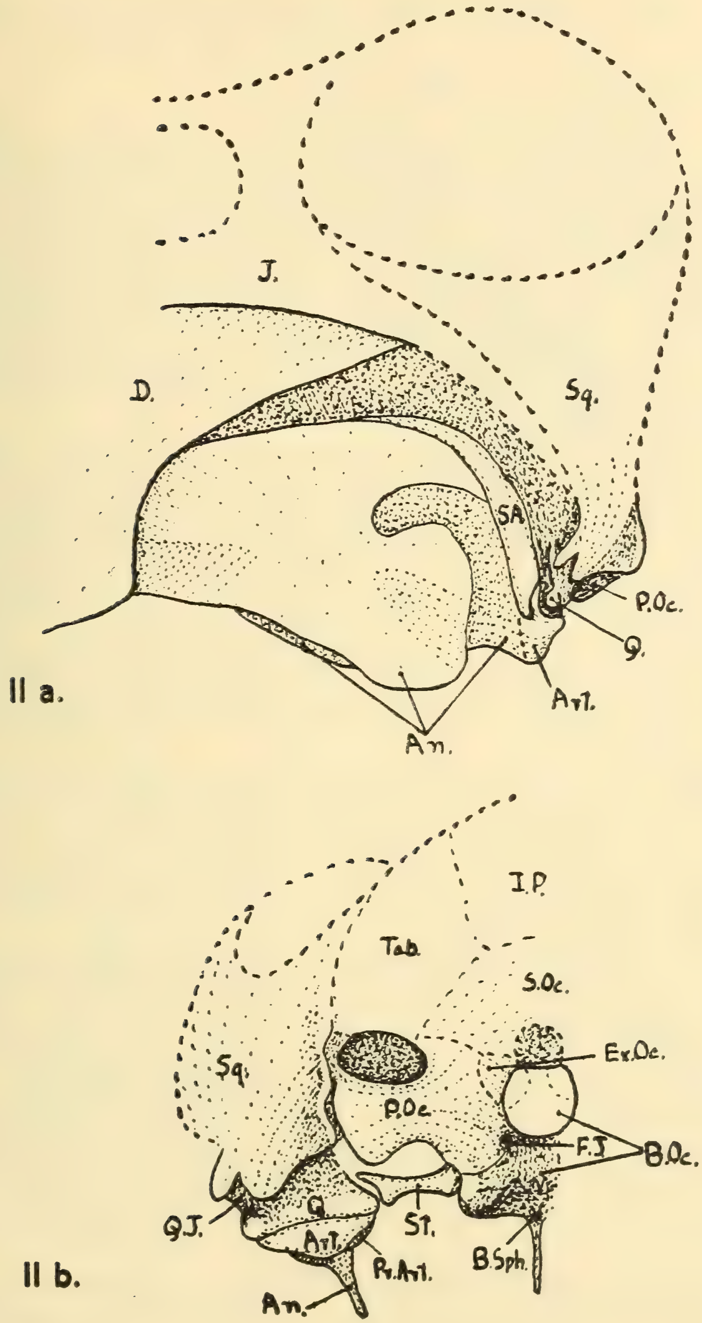


FIG. II.—*Therioides cyniscus* Gen. et Sp. Nov. S.A.M. 11888, Vindraersfontein, Beaufort West ($\times \frac{2}{3}$). *a*, lateral view. *b*, occipital view.

Anterior to the descending sheet of the squamosal the paroccipital appears to abut against the median surface of the ascending pillar of the quadrate.

THERIOIDES CYNISCUS Gen. et Sp. Nov. (fig. II)

On the farm Vindraersfontein, Beaufort West, I collected a fair skull and fore-limb which I believe to be new and for which I propose the name *Therioides cyniscus* gen. et sp. nov. and the genotype bears the S.A.M. No. 11888. This new genus may preliminarily be described as a Pristerognathid with dental formula i. 6, c. 1, p.c. 6–7, postcanines slender and small, mentum fairly strong and squarish, quadrate situated far ventrally, maximum length about 270 mm., snout as high as broad (55 mm.), orbit well in posterior half of skull.

In *Therioides* the posterior edge of the dentary sweeps sharply in posterior direction and is directed more in the direction of the squamosal than towards the dorsally situated temporal opening.

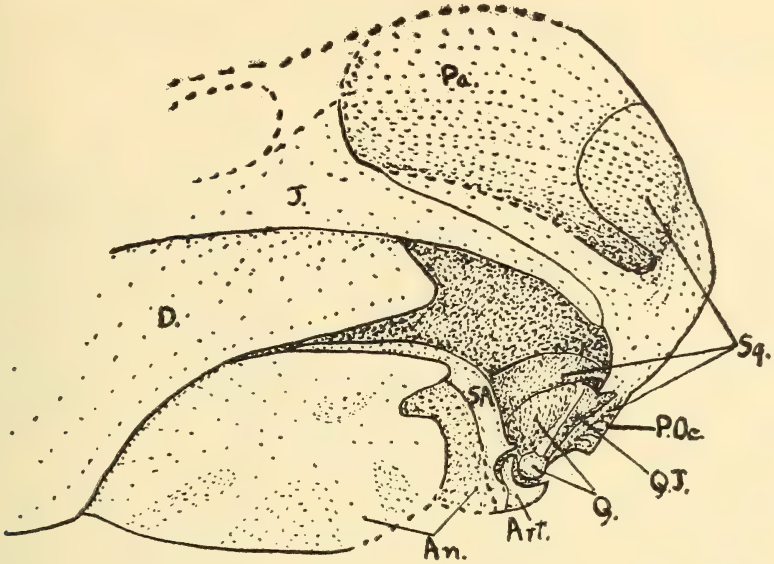
The angular has a smooth surface in its dorsal part; antero-ventrally there is a groove and another groove is directed postero-ventrally. On its lower border a thin sheet of bone lying medially projects below the edge of the outer surface. The reflected lamina is strongly developed but does not extend to the surangular. A deep notch lies dorsal to the reflected lamina and the bone surface in the notch is formed by the angular. In lateral view the surangular shows as a curved girder, anteriorly lying medially of the upper angular edge. Postero-ventrally it firmly clasps the articular. The articular is small with a slight indication of a retro-articular process. Medio-ventrally the articular is underlapped by the prearticular.

The quadrate in lateral view shows little more than the circular outline of the outer condyle above which the quadratojugal lies. In posterior view the transversely situated condylar part is partly exposed and the stout dorsal pillar-like body of the bone is seen to be overlapped by the squamosal. Medio-ventrally the rounded corner of the quadrate appears to form a surface to receive the concave distal end of the stapes.

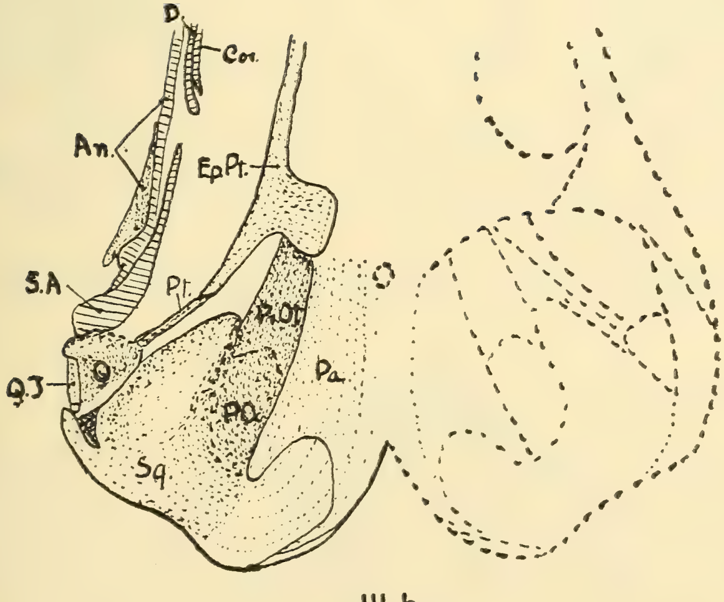
The quadratojugal is not clearly exposed but the visible bone immediately above the external rounded condyle of the quadrate is apparently the lateral part of the quadratojugal.

The postero-lateral corner of the squamosal is indentured immediately above what I believe to be part of the quadratojugal. The ventral border of the posterior descending flange of the squamosal is shallowly concave and this edge probably served for the attachment of the tympanic membrane. Lateral to where the squamosal abuts against the distal end of the paroccipital, the squamosal has a high, thin sigmoid rampart forming the median wall of the auditory groove.

The ventro-distal corner of the paroccipital has a sharp edge to which the tympanic membrane was in part attached. The stapes is a slender rod in which I have not been able to detect a foramen. Its distal end has its dorsal corner prolonged and this, tipped with an extrastapedial cartilage, was probably



III a.



III b.

Fig. III.—*Pristerognathus roggeveldensis* Sp. Nov. S.A.M. 9356*a*, Roggekloof, Sutherland (× ⅘). *a*, lateral view. *b*, dorsal view. A horizontal fracture makes it possible to remove the left temporal, post- and suborbital arches and show the underlying mandibular bones in horizontal section and a dorsal view of the quadrate and quadratojugal.

attached to the tympanic membrane, and the relative positions are such that the connection would be to the centre of the apparently circular tympanic membrane.

Pristerognathus roggeveldensis Sp. Nov. (fig. III)

Among some Pareiasaurian and Deinocephalian bones collected by Mr. A. R. E. Walker some forty years ago, I found a distorted Therocephalian skull (S.A.M. No. 9356*a*) representing a new species of Therocephalian, which I am provisionally including in the genus *Pristerognathus* although Seeley's genotype is of such a nature that identification with it as norm is hazardous. Specific characters of the new species, *roggeveldensis*, are: dental formula i. 6, c. 1, p.c. 5, maximum length of skull 255 mm., snout long, broader than high (52 : 50 mm.); orbit in posterior half of skull; dentary with truncated posteriorly directed coronoid process. Due to the distortion the subtemporal bar is pushed up revealing much of the quadrate complex which in life would be covered. The dentary has its coronoid process truncated and directed posteriorly.

The outer surface of the angular has a number of radiating ridges separated by shallow grooves. The reflected lamina does not stretch far posteriorly and the notch is shallow. In lateral view the surangular has the same girder-like shape as in the previous forms and the articular is also very similar.

In lateral view the quadrate shows the typical circular outline of the external condyle clasped by the articular. From the condyle a thin sharp ridge stretches postero-dorsally. Anterior to this ridge and lying in a more median plane the antero-lateral face of the body of the quadrate is seen with its dorsal edge overlapped by the squamosal, which here forms a domed antero-medially directed sheet of bone. Posterior to the lateral ridge on the quadrate is some bony substance which I believe represents the small splint-like quadratojugal. In dorsal view it is seen that the quadrate lies well laterally in the skull and is situated in the angle formed by the subtemporal arch and the antero-medially directed domed sheet of the squamosal lying in the posterior part of the temporal space.

The antero-medial corner of the quadrate abuts against the slender quadrate ramus of the pterygoid and in fig. III*b* its relations to the epipterygoid can also be seen.

An Unidentified Pristerognathid (fig. IV*a*)

A shepherd on the farm Dikbome, Laingsburg District, found some weathered fragments of a Pristerognathid skeleton (S.A.M. 11959). One fragment is the remains of the right articulatory region of the lower jaw. Here the quadratojugal has been lost and the lateral aspect of the quadrate is well exposed. The condylar part of the quadrate is not fully exposed but appears to be a transversely placed roller-shaped mass posteriorly separated from the ascending pillar by a well-defined groove. The condylar mass projects laterally as a process rounded

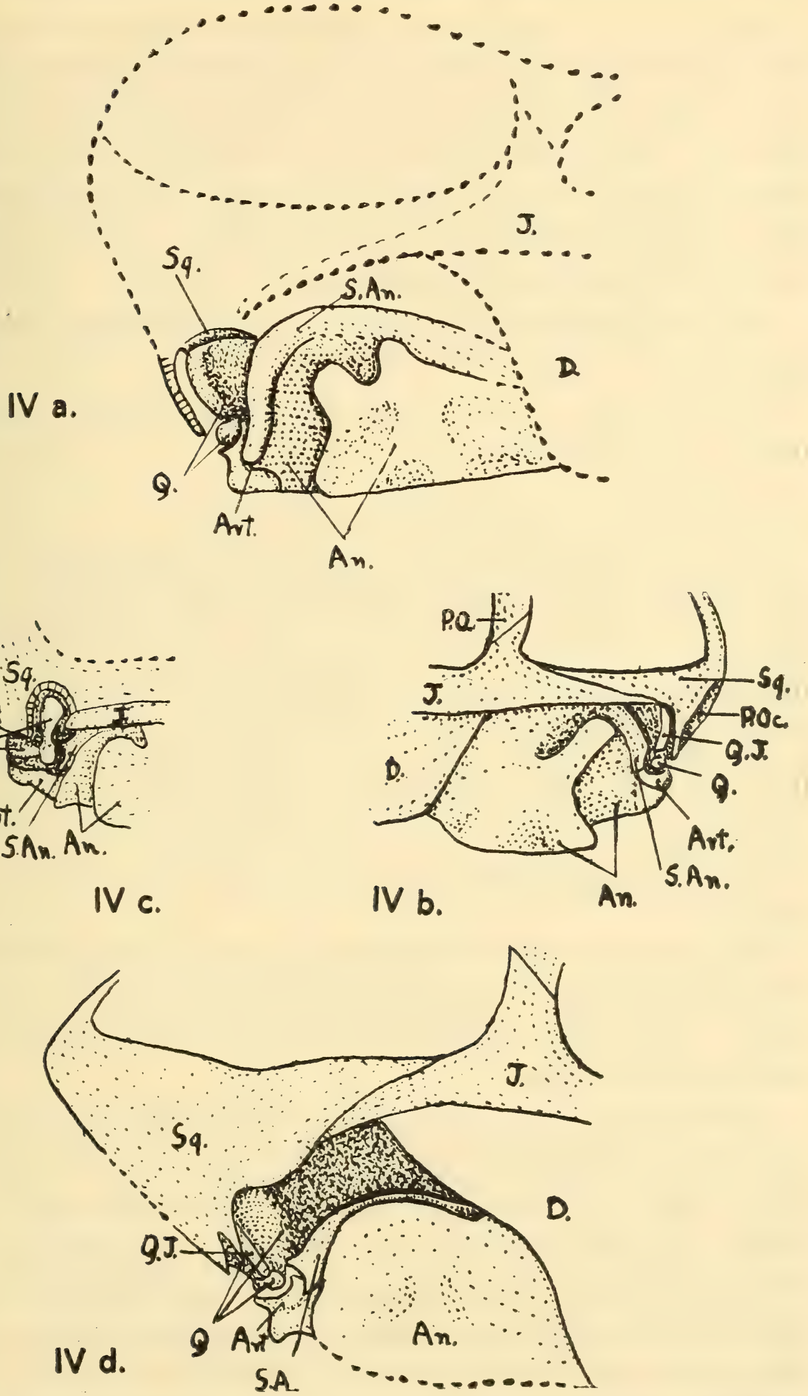


Fig. IV.—*a*, unidentified Pristerognathid. S.A.M. 11959, Dikbome, Laingsburg. Lateral view ($\times \frac{2}{3}$). *b*, *Maraisaurus parvus* Gen. et Sp. Nov. S.A.M. 11944, Buffelsvlei, Beaufort West. Lateral view. Left. ($\times \frac{2}{3}$.) *c*, *Maraisaurus parvus*. Lateral view. Right. ($\times \frac{2}{3}$.) *d*, *Alopecognathus angustioriceps* Sp. Nov. S.A.M. 9342, Kroonplaas, Beaufort West. Lateral view ($\times \frac{2}{3}$).

ventrally and dorsally hollowed out. It is in this dorsal hollow that the base of the quadratojugal must have rested. Above the external condyle the ascending body of the quadrate forms a rounded edge dorsally meeting the internally domed squamosal sheet. Anterior to this ridge the quadrate has a concave lateral face. The ascending process of the quadratojugal must have passed up along the posterior face of this ridge on the quadrate. On the antero-median lower corner of the quadrate a sectional face indicates where the pterygoid ramus of the quadrate emerged. The antero-dorsal face of the quadrate is covered by the domed sheet of the squamosal.

Posteriorly the descending sheet of the squamosal extended to the level of the upper edge of the condylar surface thus exposing little of the posterior face of the quadrate.

The relations of the angular, surangular and articular are in essentials as in the previously described forms.

MARAISAURUS PARVUS Gen. et Sp. Nov. (fig. IV*b* and *c*)

Mr. Johannes Marais, who has for a number of years been actively interested in the fossils found on his farm, has given me a small Pristerognathid skull obtained on Buffelsvlei, Beaufort West (S.A.M. 11944). Unfortunately the snout has been broken off obliquely in front of the orbits so that the nature of the dentition remains unknown, but the rest of the skull shows it to be undoubtedly a Pristerognathid. For this form I propose the name *Maraisaurus parvus* in recognition of the work of its finder. This genus is characterized by the small size of the skull (probable maximum length 162 mm.), large orbits (34×26 mm.), narrow snout, squarish in cross-section; dentary not extending far posteriorly.

The posterior border of the dentary does not curve much in dorso-posterior direction.

The angulars are not very well preserved as is evident from the differences in the figures (*a* and *b*) of the two sides. It is, however, clear that the notch is situated much dorsally and that the reflected flange does not extend far posteriorly. The relations of the surangular and articular agree in essentials with the forms described above.

On the right side the lateral surfaces of the bones forming the jaw articulation have been weathered and the quadratojugal lost. As preserved the quadrate appears to be a roughly rectangular element. The condyle is a transversely situated roller with a shallow groove demarcating two nearly equal convex surfaces. Posteriorly above the condyle there is a transverse groove medially receiving the descending plate of the squamosal and laterally the base of the quadratojugal. On the left side a weathered bony edge is preserved which in fig. IV*b* I have labelled the quadratojugal believing it to flank the quadrate edge as seen in fig. IV*a* above the outwardly directed process of the external condyle.

Alopecognathus angustioriceps Sp. Nov. (fig. IV*d*)

This new species is based on a well-preserved complete skull found by me on the farm Kroonplaas, Beaufort West (S.A.M. 9342). It differs from the genotype in its smaller size (252 mm.) and in having a more slender skull.

On the right side the articulatory region is fairly well exposed. An indentured descending sheet of the squamosal overlaps the ascending parts of the quadrate and quadratojugal. The quadratojugal has its base resting on the upper surface of the external quadratic condyle, which is much the smaller of the two parts of the condyle. In postero-ventral view the distal corner of the paroccipital, the concave squamosal edge and the internal border of the quadratic condyle form two-thirds of a circle and it is in this space where the tympanic membrane must have been situated.

The reflected flange of the angular extends to the surangular and no angular notch is present.

With the above determinations we now know that the quadratojugal does not form part of the articulatory condyle in a number and probably in all Therocephalians. In addition to the above forms a similar condition has been found by Broom in *Lycedops* and *Hyenosaurus*, and in *Trochosaurus* my figure of the occiput (*Ann. S. Afr. Mus.*, vol. XXXI, fig. 10, p. 229) falls in line with the above interpretation.

The nature of this region in Therocephalians affords further evidence for the derivation of the Cynodonts from the Therocephalians. In addition to the cynodonts hitherto known to have the same relations of the quadrate to the quadratojugal I have a cynograthid from Winnaarsbaken (S.A.M. 11264) where the quadratojugal lies well laterally to the condyle. The well-defined auditory groove of the cynodonts is undoubtedly foreshadowed in its essential relations by the less well-defined groove seen in the Therocephalians.

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ANNALS

OF THE

SOUTH AFRICAN MUSEUM

VOLUME XLII

Descriptions of the Palaeontological Material collected by the South African Museum and the Geological Survey of South Africa.

PART II, *containing:—*

ISSUED JANUARY 1954. *PRICE 15s. od.*

PRINTED FOR THE
TRUSTEES OF THE SOUTH AFRICAN MUSEUM
AND THE
GEOLOGICAL SURVEY OF SOUTH AFRICA

BY THE NATIONAL COMMERCIAL PRINTERS LIMITED,
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7. *The Pristerognathid Therocephalians from the* Tapinocephalus-*zone in the South African Museum.* By L. D. Boonstra, D.Sc.

(With 22 text-figures)

In the course of my study of the fauna of the Tapinocephalus-zone the collection of Therocephalians in the collection of the South African Museum has grown to number nearly a hundred specimens. The majority belong to the family Pristerognathidae. Unfortunately, well preserved specimens are rare and, although we have some good skulls, most of the specimens are weathered snouts and in only a few cases have we postcranial elements associated with the cranial material. In this paper I propose to deal only with the cranial material.

The Pristerognathids represent the bulk of the small to fairly large carnivores in the fauna of the *Tapinocephalus-zone.* With them occur members of some other Therocephalian families viz. Lycosuchidae and Scylacosauridae and as a lesser element some Scaloposauridae, which were probably insectivorous. The balance of the carnivorous section in the fauna is formed by a few small Gorgonopsians and then we have the large and massive Titanosuchid Deinocephalians.

The food source of these carnivores consisted mainly of the number of small herbivorous Dicynodonts and the abundant large Pareiasaurs and Tapinocephalid Deinocephalians. Some of the Pristerognathids were probably carrion eaters.

Family Pristerognathidae

Diagnosis

Fairly small to large early carnivorous Therocephalians from the *Tapinocephalus-zone* with a dental formula varying within the limits, i.$\frac{5-6}{3}$, c.$\frac{1}{1}$, p.c.$\frac{2-9}{2-9}$. The incisors and canines usually well developed and the post-canines, with few exceptions, relatively feebly developed. Skull long, fairly high and narrow; snout long, fairly narrow; sagittal crest high and sharp; temporal fossa moderately long and broad; low to fairly low over post-orbital arches; lower jaw strong, dentigerous ramus of dentary not curved and relatively long, post-dentary part of mandible strong, strong coronoid process. Prefrontal and postorbital well developed; and postfrontal well to fairly well developed; jugal arch moderate to strong; frontal with moderate entry into orbital border or excluded from it; septomaxilla with well developed facial surface; pineal foramen medium to

fairly large; parietal narrow with sharp crest; paroccipital strong; occiput fairly high and broad, deeply concave; epipterygoid narrow; anterior palatal openings medium to long; suborbital vacuities large; palate flat; with only the anterior ramus of the pterygoid bearing teeth; basisphenoidal tubera of medium size, parasphenoidal keel deep; suspensorium posteriorly situated high up and only moderately laterally displaced.

Within the family two groups can be recognised which may yet have to be considered as subfamilies:

a. Those with 6 incisors and with skulls where the length is double or more the breadth.

b. Those with 5 incisors or with an inconstant 6th and where the skull length is less than double the breadth.

General Description

Incisors, canines and post-canines have a sharp posterior cutting edge which is serrated — the serrations vary from fine to fairly coarse. The incisors are moderately curved teeth with a more or less flattened extremity forming a curved cutting edge. They vary from fairly weak to very strong seizing and tearing teeth. The first incisor with its fellow form a pair of teeth closely set to each other, with the root rounded in cross section and always smaller than the second incisor. The second to the 5th incisor are subequal or decrease in size backwards. In the forms with six incisors the 6th tooth is inconstant in some genera and in the others it is mostly much smaller and weaker than its predecessors. There is always only one canine; except in one genus the canine is always a strong curved dog-tooth with its extremity more pointed than is the case in the incisors; the upper canine is situated far forward in the maxilla (except in one species) and to house its long strong root the maxillary edge has grown downwards so that the premaxillary edge is situated at a higher level; usually the alveolar border curves evenly upwards anterior to the canine, but in some the transition is by a distinct step. The diastema between last incisor and canine varies considerably in length — sometimes the canine follows immediately after the last incisor. Behind the canine the diastema to the first postcanine also varies considerably, but only in one specimen does the first postcanine lie right up against the canine.

The number of postcanines varies considerably in the Pristerognathids — from 2 to 9. The postcanines of the family, considered as a group, must be described as weakly developed. They are usually small slightly curved teeth either closely set or well spaced. In only one genus *(Cynariognathus)* do they form a set of well developed teeth. They are often irregular and of little functional importance.

In the dentary there are apparently always 3 incisors, which in the closed jaws are overlapped by the upper incisors. The lower canine lies lingually

and anteriorly to the upper canine and its point in the closed jaws is housed in the anterior section of the "choanae". Little is known of the postcanines of the dentary — they lie lingually to those of the maxilla.

It is thus evident that the Pristerognathids in their feeding relied on the anterior part of the jaws; the large canine acting as piercing instrument to effect the kill and these together with the incisors were used to hold the victim and then acted as the instruments for tearing away pieces of flesh. Those with weaker incisors were probably carrion eaters. In most Pristerognathids the postcanines acted chiefly as protruding points preventing flesh from slipping out of the mouth. The transverse pterygoidal rami limited the action of the lower jaw to movement in a vertical plane and there was thus no chewing or cutting by the postcanines. The small set of recurved teeth on the pterygoidal ridge served to hold the flesh in the stage preliminary to deglutition.

The postfrontal is well developed in some species, whereas in others it is only a fairly small splintlike bone; it has only a small posterior extent, in some forms extending up to the plane of the fronto-parietal suture, in others a little further and at most to the level of the pineal foramen. It seldom extends further posteriorly than the postorbital. The posterior tongue is usually confined to the dorsal surface but sometimes lies on the lateral face of the parietal crest.

The postorbital varies in the extent of its participation in the postorbital bar, which is slender to fairly slender, never widened; in some forms it has a small entry into the orbital border and the temporal border; in others the entry into the orbital border is small, but the entry into the temporal border is large; this depends on how high the dorsal jugal ramus extends and to what extent the jugal is confined to the posterior half of the postorbital bar. A postero-dorsal tongue of the postorbital sometimes just enters the supratemporal border where it is applied to the lateral face of the parietal or it sometimes develops quite a fair-sized sheet of bone flanking the parietal, but seldom extends to just behind the plane of the pineal foramen.

The jugal is always well developed; it is triradiate with a dorsal, anterior and posterior ramus. The anterior ramus forms the lower part of the orbital border and a varying portion of the lower part of the posterior orbital border; it mostly forms a sharp pointed wedge in between the lacrimal and maxilla, but this is sometimes truncated. The dorsal ramus sometimes forms the whole posterior half of the postorbital bar and thus this part of the temporal border; in other forms its dorsal extent is much smaller and this part of the temporal border is formed by the postorbital. The posterior ramus always extends very far posteriorly as a long pointed wedge underlying the anterior ramus of the squamosal, together forming the temporal arch. Usually the jugal forms nothing or very little of the upper border of the temporal arch, but in those forms where the anterior ramus of the squamosal is short it forms the anterior

portion of the upper border of the temporal arch. (This long posterior ramus of the jugal in the Pristerognathids resembles the condition seen in Cynodonts much more than does the jugal of the Gorgonopsians.)

The squamosal is always well developed; it has an anterior ramus extending far anteriorly to form most of the upper border of the lower temporal arch where it overlies the jugal; its ventral ramus extends far ventrally, laterally largely covering the quadratojugal and posteriorly covering most of the posterior face of the quadrate, which is housed in a recess in the antero-ventral face of the descending ramus of the squamosal; the medially directed ramus of the squamosal forms the posterior border of the temporal fossa and is here applied to the outer face of the parietal; this overlap of the squamosal on the parietal is fairly small so that the postorbital and squamosal only flank the lateral face of the parietal in its extreme anterior and posterior part respectively, leaving the parietal to form nearly all of the upper border of the temporal fossa. Where the squamosal meets the strong paroccipital the edge of the squamosal is everted to form the auditory groove. The sweep of the squamosal posteriorly carries the posterior border of the temporal arch far back in the long narrow headed forms and thus forms a deeply concave occiput, whereas in the shorter broader-headed forms there is only a moderate backward sweep with a shallowly concave occiput. There is only a moderate lateral sweep of the squamosal so that the temporal fossa never becomes very wide. There is more lateral sweep in those forms where the posterior sweep is least.

In dorsal view the Pristerognathids show little more of the upper occipital bones than their dorsal edges; the occiput is thus upright. In many forms the condyle is clearly visible in dorsal view, but in the longheaded forms it is either just visible or just hidden by the backward sweep of the parietals.

The quadratic condyles lie well below the level of the occipital condyle and in a plane well below that of the alveolar border of the maxilla; they have migrated very little in lateral direction so that the outer edge of the quadrate ramus of the pterygoid is fairly straight; there has also been no forward migration and they still occupy a posterior position.

The quadratojugal is much reduced and is a small element not entering the condylar surface but resting with its base on the ledge of the quadrate above the outer part of the condyle and with two weak dorsal processes fitting into recesses in the overlapping squamosal.

The large prefrontal has a rounded ridge separating a dorsal from a lateral face, but farther anteriorly the snout is rounded with no abrupt transition from dorsal to lateral surface.

The lacrimal is small and has little anterior extension due to the upward growth of the maxilla; it lies in the preorbital depression which is usually fairly shallow and extending as a shallow groove in the direction of the canines; but in some forms this depression is deep with sharp margins and

anteriorly ends abruptly. The homology of the gland occupying the preorbital depression is uncertain.

The long and strong root of the canine is housed in a strong rounded bulge of the maxilla, which is consequently a high bone. The outer surface of the maxillary bulge often has an ornamentation of sub-crocodilian pitting, but in some forms it appears to be fairly smooth. It is pierced by a number of nutritive foramina.

The nasals are long and fairly narrow; together they are hourglass-shaped; the constricted waist being due to the upward growth of the maxilla overlapping the lateral edge.

In the lower jaw the symphysis is always weak and unankylosed, with the splenial just entering the symphysis and forming a very subordinate part and not visible ventrally. The angular has a large outer face with a notch and a reflected lamina.

Systematic Descriptions

Genus *Scymnosaurus* Broom.

Broom, 1903, p. 152. Genotype, *S. ferox* Broom.

Large Pristerognathids with dental formula i.5, c.1, p.c.2-4; incisors and canines large and strong, postcanines fairly weak to medium, varying in number — 2, 3 or 4. (In one specimen a small 6th incisor has been seen, but only on the one side.)

Skull very large (Max. Length 375 to 475 mm.); preorbital hollow fairly shallow, not sharply demarcated and really not more than a groove stretching from the orbit in the direction of the canine; septomaxilla and septomaxillary foramen well developed; frontal either excluded or possibly just entering the supraorbital border; snout probably always slightly broader than high, slightly narrowed between orbits and canines; orbits partly in anterior half of skull.

Mandibular symphysis, formed solely by dentaries, weak, unankylosed, mentum sloping little or moderately.

Scymnosaurus ferox Broom. (Figs. I, IIa.)

Broom, 1903, p. 152. Holotype. S.A.M. 632. Locality unknown. Coll. unknown. A well preserved but imperfect snout.

There are 3 to 4 postcanines; mentum moderately sloping and symphysis weak; maximum length of skull 375 to 381 mm. (as reconstructed); frontal possibly still entering orbital border.

S.A.M. 632 (Fig. 1*a*).

Broom's holotype consists of the anterior third of the mandibular ramus, the dentigerous border of the premaxillaries and the maxillaries up to just behind the 3rd postcanine on the right and the 2nd postcanine on the left side. The horizontal fracture through the snout shows the dorsal surface of the anterior third of the palate, which is as figured by Broom (1903, Pl. 18, fig. 9).

The first four incisors are strong, whereas the 5th is much shorter and this tooth shows fine serrations on its sharp posterior edge; the robust canine has fine serrations on its sharp posterior edge; only 3 postcanines are preserved and these decrease rapidly in size in posterior direction; the postcanines bear coarser serrations on the posterior edge.

Referred Specimens

S.A.M. 3430 (Fig. 1*b*). Janwillemsfontein, Prince Albert. Coll. Haughton & Whaits.

This is an imperfect snout in which is preserved the symphysis and the major part of the premaxillaries and maxillaries. In both premaxillaries 5 incisors are preserved and here the 5th is only slightly shorter than the anterior 4 incisors. But on the left side there is a stump of what appears to be a small 6th incisor. On the right side a stump of the canine is preserved, as also stumps of the 2nd and 4th postcanines and empty alveoli of the 1st and 3rd. On the left side the canine has dropped out and so has the 1st postcanine, but stumps of the 2nd and 3rd are preserved.

The maxilla overlaps the premaxilla right up to the level of the anterior edge of

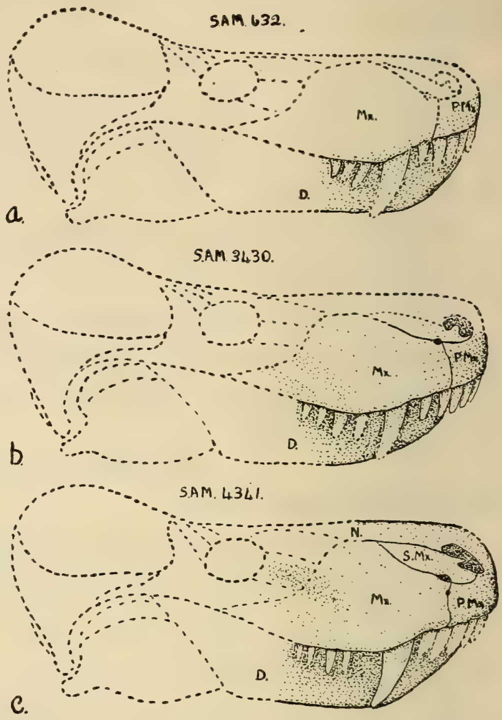


Fig. 1.—*a*, *Scymnosaurus ferox*. Type. S.A.M. 632. (× $\frac{1}{6}$.) Right side of snout fragment. *b*, *Scymnosaurus ferox*. S.A.M. 3430. (× $\frac{1}{6}$.) Right side of snout fragment. *c*, *Scymnosaurus ferox*. S.A.M. 4341. (× $\frac{1}{6}$.) Right side of snout.

Lettering of Figures: A.—angular; Art.—articular; B.O..—basioccipital; B.S.—basisphenoid; D.—dentary; Ep. Pt.—epipterygoid; Ex.—exoccipital; F.—frontal; F.J.—foramen jugale; F.O. fenestra ovalis; I.P.—interparietal (postparietal); J.—jugal; L.—lacrimal; Mx.—maxilla; N.—nasal; P.—parietal; Pal.—palatine; P.F.—prefrontal; P.Mx.—premaxilla; P.O.—postorbital; P.Oc.—paroccipital; Po.F.—postfrontal; Pr.Ot.—proötic; P.S.—parasphenoid; Pt.—pterygoid; P.V.—prevomer Q.—quadrate; Q.J.—quadratojugal; S.A.—surangular; S.Mx.—septomaxilla; S.Oc.—supraoccipital; Sq.—squamosal; St.—stapes; Tab.—tabular; Tr.—transversum.

The figures are orthoprojections taken with a pantograph and, except where specifically stated, they are of the specimens as preserved without correction of any distortion. Reconstructed parts and uncertain features are shown in broken line. All figures drawn by the author.

the 4th incisor. The bulge of the maxilla above the canine is rugosely pitted, but no nutritive foramina can be seen. The septomaxillary foramen is of moderate size (6 mm.).

S.A.M. 4341 (Fig. 1*c*). Stinkfontein, Prince Albert. Coll. Haughton.

This is a weathered snout bleached white. Each premaxilla has the stumps of 5 incisors preserved; in cross section the 5th is only slightly smaller than the 4th; in the right maxilla imperfect crowns of 4 postcanines are preserved; the 3rd and 4th are the smallest and the 2nd the largest maxillary tooth.

The septomaxilla has a large facial exposure and a stout spur directed anteriorly into the nostril. There is a fairly large oval septomaxillary foramen and in the maxillary edge, greatly overlapping the premaxilla, there is a nutritive foramen. The maxillary bulge is rugosely sculptured. The nasals broaden as they approach the nostril.

S.A.M. 9084 (Fig. 2*a*). Rietkuil, Beaufort West. Coll. Boonstra.

This specimen consists of the major part of a distorted skull, lacking the intertemporal region, together with the ends of a humerus, radius and ulna. The articulatory region has recently been described and figured (Boonstra, 1953, fig. 1).

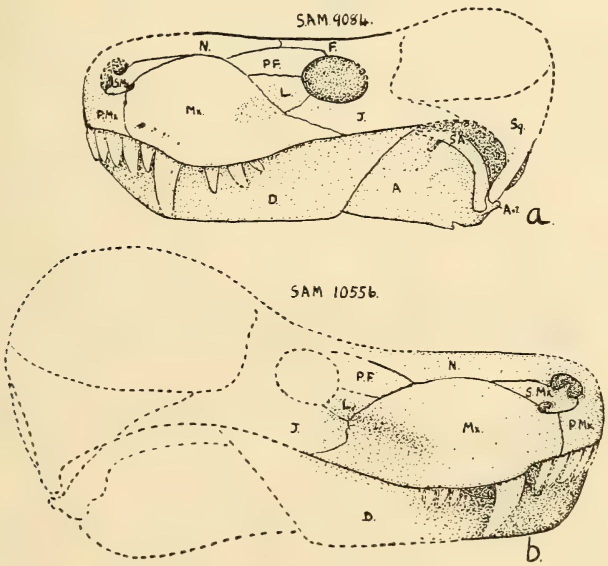


FIG. 2.—*a*, *Scymnosaurus ferox*. S.A.M. 9084. (× ⅙.) Left side of skull and lower jaw with correction of the distortion. *b*, *Scymnosaurus major*. S.A.M. 10556. (× ⅙.) Right side of preorbital part of skull.

With the full length of the lower jaw preserved it is possible to estimate the maximum length of the *Scymnosaurus ferox* skull viz. 375 mm. The incisors are large and robust with the 5th only slightly smaller than its predecessor and the sharp posterior edge bears moderately fine serrations. The 3 postcanines are short stout teeth with the 3rd much smaller than the anterior ones and the serrations on the posterior edge are as in the incisors and the canine. The 5th incisor lies close to the canine, whereas in the specimens mentioned above there is an appreciable diastema.

The preorbital depression has clearly demarcated borders.

The maxillary bulge is pitted and is perforated by a number of nutritive foramina. The septomaxillary foramen is fairly large (6 mm.) and the septomaxilla well developed but with less facial exposure than in S.A.M. 4341.

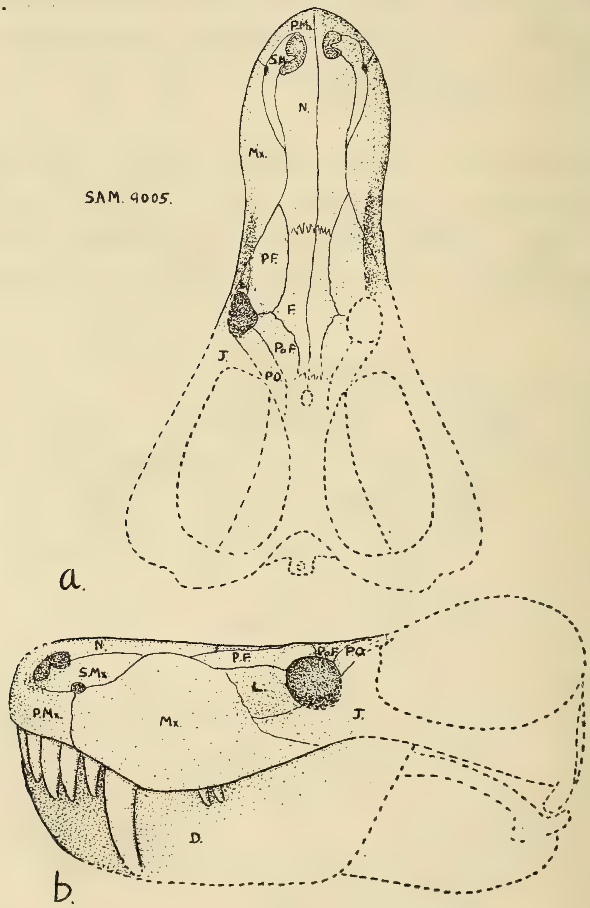


FIG. 3. *Scymnosaurus major*. Type. S.A.M. 9005. (× 1/6.) *a*, Dorsal view. *b*, Left side.

The orbit lies partly in the anterior half of the skull.

The dentary is strong, with a straight ventral edge, a sloping mentum and a weak symphysis.

S.A.M. 4341.

Scymnosaurus major. Sp. Nov.

Holotype. S.A.M. 9005. Klein-Koedoeskop, Beaufort West. Coll. Boonstra.

The well preserved anterior two thirds of a skull together with parts of the pectoral and pelvic girdles, ends of humerus and radius and ulna.

There are 2 to 3 postcanines; mentum fairly upright and symphysis fairly strong; maximum length of skull 450 to 474 mm. (as reconstructed); frontal excluded from orbital border.

S.A.M. 9005 (Fig. 3 *a* and *b*).

The estimated maximum length of the skull is 450 mm. The incisors are large and strong (length of 3rd incisor 55 mm.); the length of the canine is 80 mm. (as reconstructed), whereas the two postcanines are small (15 mm.). All the teeth have a finely serrated sharp posterior edge. The 5th incisor lies close up to the canine, but the distance between the canine and the first postcanine is large (30 mm. on the right side and 50 mm. on the left).

The preorbital depression is deep but with rounded margins.

The maxillary bulge has pronounced pits and radiating grooves. The septomaxilla is well developed and the foramen fairly large (11 mm.). The maxilla is high but short.

The nasals widen considerably in their anterior half.

The frontals are small, very narrow and well removed from the orbital border. The prefrontals are large and the postfrontals fairly large.

The orbits are small and round (45 mm.) and lie partly in the anterior half of the skull.

The mentum is fairly upright but the two rami are loosely joined at the symphysis.

S.A.M. 10556 (Fig. 2*b*). Knoffelfontein, Beaufort West. Coll Boonstra.

This specimen consists of a weathered and bleached preorbital part of a large skull (474 mm. as reconstructed). Only cross sections of the roots of the teeth are preserved. The five incisors are practically of equal size.

Anterior to the canine there is a distinct diastema and the edge of the maxilla curves sharply downwards (the "step" of Watson). Posterior to the canine there is a diastema of 27 mm., then follow three closely packed small postcanines.

The preorbital depression forms an oblique groove from the orbit in the direction of the canine.

The maxillary bulge is strongly pitted. The septomaxilla is well developed with a strong intra-nostril spine. The septomaxillary foramen is very large (19 mm.) and is kidney shaped with a spur from the septomaxilla dividing it into two, in very much the same way as the medially directed spine divides the nostril.

The maxilla is low and fairly long.

The mentum is upright and the symphysis quite strong.

SCYMNOSAURUS sp. INCERTAE SEDIS

The following fragmentary specimens can be referred to the genus but specific determination is uncertain.

S.A.M. 8999. Locality unknown. Coll. unknown. A weathered snout fractured cleanly just behind the canines and from which little more can be determined than that there were 5 large subequal incisors and a fairly strong canine.

S.A.M. 11459. Buffelsvlei, Beaufort West. Coll. Boonstra and Marais. A weathered snout in pieces, with the dental formula i.5, c.1., p.c.3+? together with parts of a carpus and tarsus.

S.A.M. 11833. Lammerkraal, Prince Albert. Coll. Boonstra and Pienaar. A weathered snout with 1 postcanine on the right side and 2 on the left.

S.A.M. 11961. Dikbome, Laingsburg. Coll. Boonstra. A weathered snout with dental formula i.5, c.1, p.c.1+?.

S.A.M. 9126. Voëlfontein, Prince Albert. Coll. Boonstra. This consists of a fairly well preserved snout with the teeth of the left side preserved i.5, c.1, p.c.3+. The teeth are very similar to those of the genotype. Being only $\frac{2}{3}$ the size of the genotype this snout may represent a small species of *Scymnosaurus*.

Genus *Scymnosaurus:* Measurements in Mms.

		S. ferox.				*S. major.*	
		632	3430	4341	9084	9005	10556
Pr.Mx. — Post.Sq. edge . .		375?	375?	381	375	456?	474?
Pr.Mx. — Ant.Orb. border .		—	—	—	187	215	216?
Width of Snout over Canines .		105?	106	105	100?	115	100
Width Interorbital		—	—	—	60?	72?	—
Height of Snout at Post. edge of Canine		90?	96?	105?	100?	110	90
Length of Upper Incisor Series	l.	65	75	65	70	85	60
	r.	60	70	60	70	75	60
Diastema C.—I.	l.	9	—	15	3	6	18
	r.	7	11	16	5	9	16
Diastema C.—P.C.	l.	14	—	—	20	51	—
	r.	14	—	24	20	27	25
Length of P.C. Series . .	l.	—	—	—	42	18	—
	r.	30	—	41	36	21	30
Ant.-Post.Diam. of Canine	l.	22	—	25	24	31	25
	r.	22	20	20	—	26	25

Genus *Glanosuchus* Broom.

Broom, 1904, p. 85. *Genotype G. macrops* Broom.

Large Pristerognathids with dental formula i.5+1, c.1, p.c.5; the first 5 incisors are large but the 6th is inconstant and when present very small; the canine is large and strong; the postcanines are moderately to weakly developed.

Skull large (Max. length 315-321 mm.); preorbital hollow fairly shallow, not sharply demarcated and really not more than a groove stretching from the orbit in the direction of the canine; septomaxilla and septomaxillary foramen well developed; frontal enters orbital border; postfrontal quite well developed; snout broader than high, slightly narrowed between orbit and canines; orbits well in posterior half of skull.

Mandibular symphysis formed solely by dentaries, weak, unankylosed, mentum sloping.

Epipterygoid only slightly widened. Sagittal crest of parietals only moderately high but fairly sharp.

Glanosuchus macrops Broom. (Figs. 4 and 5.)

Broom, 1904, p. 85. Holotype. S.A.M. 637. Knofloksfontein, Beaufort West. Coll. Snyman.

A well preserved skull lacking only the posterolateral corners of the skull and thus the suspensorial region.

Broom's description was based on the only partially cleaned skull. I have cleaned up the outer surface, thus revealing the sutures and prepared the palate and basicranium so that these features can now be described.

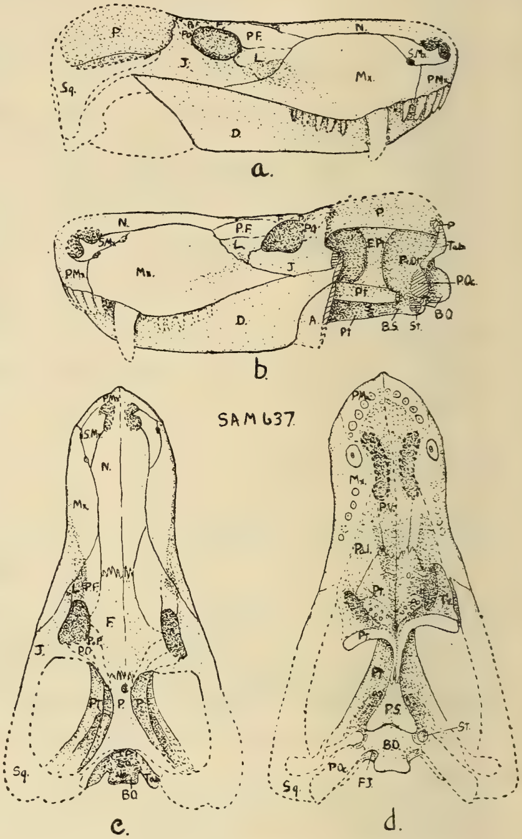


FIG. 4.—*Glanosuchus macrops*. Type. S.A.M. 637. ($\times \frac{1}{6}$.) *a*, Right side. *b*, Left side. *c*, Dorsal view. *d*, Ventral view.

In Fig. 4 *a, b* and *c* the structural features of the lateral and dorsal surfaces are shown. The septomaxilla has a large facial exposure, the spur projecting into the nostril is well developed and the foramen fairly large (6 mm.). The maxilla is fairly high and long with its dentigerous border curving upwards anterior to the posterior edge of the canine. The preorbital hollow has a fairly definite dorsal and posterior rim but anteriorly it flows into the general maxillary surface in the direction of the canine. The maxillary bulge above the canine is fairly smooth. The nasals are widest anteriorly. The frontal is of medium size apparently just entering the orbital border. In dorsal view the occiput is seen to be deeply concave. In outline the epipterygoid is hourglass-shaped and although not much widened it is not a columnar *columella cranii*. Its base, resting on the quadrate ramus of the pterygoid, has no great posterior process. Although the edge of the sagittal crest is not preserved it is clear that the crest was not very high and moderately sharp. The temporal fossa is short but roomy.

The ventral surface (Fig. 4*d*). With the dentaries in occlusion it has not been possible to expose the choanal region. The prevomers posteriorly form a truncated spatulate sheet of bone underlying the median edges of the palatine and the anterior edge of the anterior pterygoidal ramus. The lateral edge of the prevomer lies medial to an oblique ridge on the palatine. This ridge is continued on the pterygoid where it is dentigerous (a cross section of

at least one tooth is clearly visible). The palatine is a relatively small bone, anteriorly bounding the choana and posteriorly forming the front margin of the oval shaped large suborbital vacuity. Two oblique sutures, meeting in an obtuse angle, separate the palatine from the prevomer and pterygoid. The pterygoid is a typically tetraradiate bone; the anterior ramus with its fellow, forms the lozenge-shaped middle part of the palate; anteriorly, between the two diverging dentigerous ridges, a V shaped hollow extends on to the prevomerine surface where it shallows and fades out; laterally the anterior ramus forms the inner border of the suborbital vacuity; the posterior part of the anterior ramus carries a prominent oblique ridge stretching from near the median line to near the edge of the suborbital vacuity; this ridge is dentigerous, carrying small sharp teeth irregularly arranged in two rows; in the median line just posterior to these dentigerous ridges there appears to be a small interpterygoidal slit.

The transverse pterygoidal ramus forms a strong bar which laterally descends to the level of the lower dentary border and this distal end lies just median to the angle of the dentary. The movement of the lower jaw is thus guided and confined with little lateral play allowed. Against the lateral part of the anterior face of the transverse pterygoidal bar lies the transversum; from here the transversum ascends rapidly and curving forwards as a thin process forms the lateral edge of the suborbital vacuity and meets the palatine.

The posterior ramus of the pterygoid with its fellow forms a median keel which clasps the anterior end of the parasphenoidal rostrum.

The quadrate ramus of the pterygoid is not completely preserved and one does thus not know whether it met the quadrate or not. On its upper surface the quadrate ramus carries the base of the epipterygoid. I have not been able to determine whether the epipterygoid has a posteriorly directed process running along the quadrate ramus. In ventral view it is seen that the edge of the quadrate ramus is only slightly concave and the epipterygoid has a roomy *cavum epiptericum* median to it and the anterior part of the proötic.

The parasphenoid is in ventral view seen as a sheet of bone underlying the basisphenoidal tubera and narrowing anteriorly is clasped by the pterygoids where these bones form a fairly deep median keel.

Ventrally the occipital condyle is formed by the strong basioccipital. Postero-laterally to the basisphenoidal tuber lies the *fenestra ovalis* with the proximal end of the stapes *in situ* on both sides. The rim of the fenestra is formed postero-laterally by the opisthotic, postero-medially by the basioccipital, antero-medially by the basisphenoid and antero-dorsally by the proötic.

Only part of the occiput is preserved; above the foramen magnum the occiput is deeply excavated; the posttemporal fenestrae are large; the

paroccipital (opisthotic) strong and only the dorsal edge of the interparietal and tabular seen on the dorsal surface.

S.A.M. 11843. (Fig. 5*a* and *b*.) Lammerkraal, Prince Albert. Coll. Boonstra.

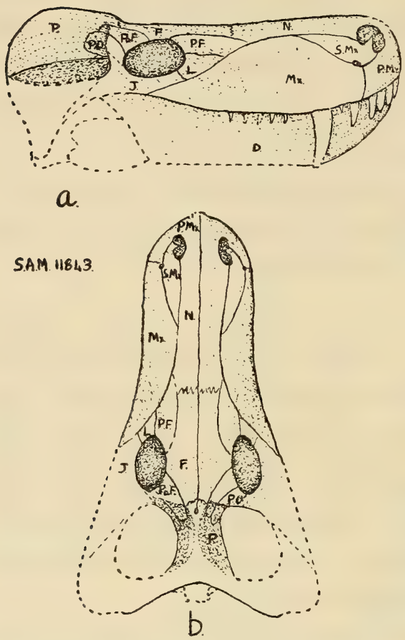


FIG. 5.—*Glanosuchus macrops*. S.A.M. 11843. (× 1/6.) *a*, Lateral view. *b*, Dorsal view. Left side incorporating features determined of the right side.

This good specimen consists of the major part of a skull lacking only the suspensorial region and the lower edge of the dentary. It is complementary to the holotype skull in that it shows that the frontal has a small entry into the orbital border, the postfrontal and postorbital flank the parietal for a short distance within the temporal fossa; the sagittal crest of the parietals is preserved as a not very high but fairly sharp crista; the temporal fossa is short but roomy. But the postcanines are smaller and more slender although in both skulls they occupy the same space (48 mm.). The 6th incisor is preserved on the right side and here also it is very much smaller than the anterior incisors. As in the type all the teeth have a finely serrated posterior border. The occiput is less deeply concave than in the type skull. The preorbital depressien is very shallow and the maxillary surface smooth over the bulge where the long canine root is housed.

S.A.M. 11964. Locality unknown. Coll. unknown.

This is a weathered snout showing the upper dentition to be i.5+1, c.1, p.c.2+?, with the 6th incisor very small as in the two foregoing specimens. Although appreciably smaller than the type the dentition agrees well with that of the type so that I am referring it to the species *macrops*.

S.A.M. 903. Seekoeigat, Prince Albert. Coll. Du Plessis.

A very much weathered snout, which on account of the presence of a small 6th incisor can be included in the genus *Glanosuchus*.

Genus *Ptomalestes*. Gen. Nov.

Fairly large Pristerognathids with the dental formula i.5, c.1, p.c.6; the incisors are subequal and fairly weak, the canine strong and the postcanines small slender teeth well spaced.

Skull fairly large (Max. Length 258 mm.); preorbital depression fairly deep but without abrupt margins and shallowing in the direction of the canine; frontal just entering orbital border; postfrontal quite well developed; snout broader than high, only slightly narrowed between orbit and canine; orbits well in posterior half of skull.

Mandibular symphysis formed solely by dentaries, weak, unankylosed, mentum sloping.

Sagittal crest of parietals only moderately high and narrow.

Ptomalestes avidus Sp. Nov. (Fig. 6*a—d*.)

Genotype. S.A.M. 11942. Steenboksfontein, Laingsburg. Coll. Boonstra.

A fairly well preserved skull, but it has been subjected to a slight shear and some weathering, together with some cervical vertebrae, part of the pectoral girdle, humeri, radii and ulnae.

In lateral view (Fig. 6*a*) the maxilla is seen to be low and long and has a long overlap on the premaxilla; the small slender post-canines are irregularly spaced and occupy 51 mm. with a diastema of 12 mm. to the canine; anterior to the canine the maxillary edge curves upwards ("step" of Watson) and the diastema is 13 mm. on the left and 15 mm. on the right side. On the premaxilla there are 5 incisors, fairly small and all more or less the same size. All the teeth have serrated sharp posterior edges.

The prefrontal is large with a dorsal and a lateral face.

The jugal has a stout dorsal ramus forming the lower and hind part of the postorbital bar; the posterior ramus extends moderately far backwards underlying the anterior

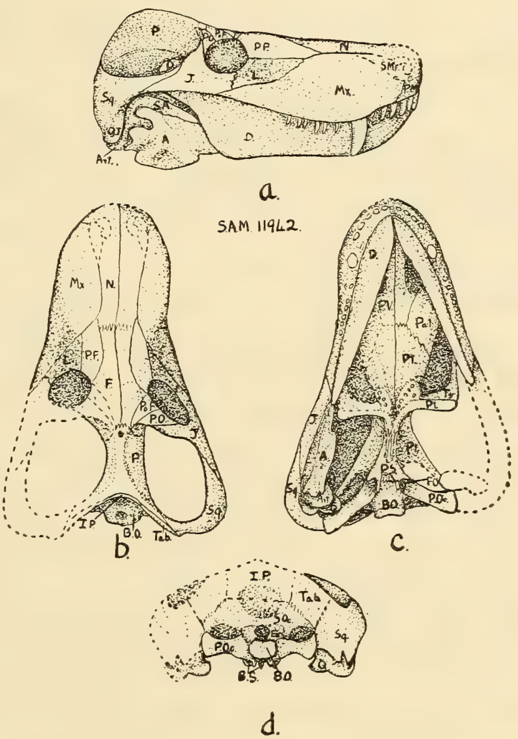


Fig. 6.—*Ptomalestes avidus*. Type. S.A.M. 11942. (× $\frac{1}{6}$.) *a*, Lateral view. *b*, Dorsal view. *c*, Ventral view. *d*, Occipital view.

part of the anterior squamosal ramus forming the infratemporal arch; the anterior jugal ramus is short.

The postorbital is of moderate size forming the postero-dorsal corner of the orbital border and has only a short posterior tongue applied to the lateral face of the parietal.

The squamosal has a deep descending process to hold and support the quadrate and quadratojugal, but I have not been able to determine the relations of these three bones as seen in lateral view.

The temporal fossa is short but roomy.

The angular has a fairly large external face with radiating ridges and posteriorly a deep notch and a well developed reflected lamina with a thin ventral edge. The surangular forms, in lateral view, the dorsal girderlike border of the jaw between the dentary and the articular. The lower edge of the dentary is straight and the posterior edge concave between the angle and the strong coronoid process, which, extending into the temporal fossa, stands out well dorsal to the surangular and the dentigerous border of the dentary.

In dorsal view (Fig. 6*b*) the parietals are seen to form a moderately high, fairly sharp sagittal crest. The frontal is fairly short, narrow and is practically excluded from the orbital border. The postfrontal is quite well developed and the prefrontal has a large dorsal surface. The occipital edge is fairly deeply concave with only the dorsal edges of the interparietal and tabulars seen in dorsal view, but the posttemporal arch does not sweep very much in posterior direction. The temporal fossa is short but wide.

In ventral view (Fig. 6*c*) the dentaries are in position so that the anterior and lateral portions of the palate are not exposed. The choanal openings are short and the interchoanal bar formed by the prevomers stout. Posteriorly the prevomers form a truncated spatulate sheet of bone underlying the palatines and pterygoids. The palatine is of fair size with its outline roughly that of a parallelogram; it carries an oblique ridge which is continued on the pterygoid. The anterior pterygoidal rami form a median flat surface laterally bounded by the above mentioned oblique ridges; no teeth can be seen on these ridges; laterally the pterygoid bounds the large suborbital vacuity; posteriorly the anterior ramus carries an eminence in which a number of small teeth are implanted mainly in a curved row. The transverse pterygoidal ramus forms a moderately strong bar inclined ventrally in lateral direction; its corner does not descend so far as the ventral edge of the dentary where this forms its obtuse angle. Posteriorly the pterygoid clasps the anterior process of the parasphenoid and forms the lateral sheets of bone of the fairly deep median keel. The quadrate ramus of the pterygoid has a fairly straight lateral edge, well removed from the braincase, and meets the quadrate.

I have not been able to determine the relations of the epipterygoid to the quadrate ramus of the pterygoid.

The transversum is biramic; a transverse ramus is applied, as a vertical sheet of bone, to the anterior face of the transverse pterygoidal ramus; a longitudinal ramus forms a girder, ascending in the skull in anterior direction to meet the palatine at its junction with the maxilla, and laterally bounding the large suborbital vacuity.

The parasphenoid forms a fairly deep median keel anteriorly clasped by the pterygoids, and presumably forms the underface of the basisphenoidal tubera. The basisphenoidal tubera are situated well below the level of the basioccipital condyle; their posterior borders are developed as a sharp ridge forming the anterior part of the deep rim bounding the *fenestra ovalis;* the medial part of the rim of the fenestra is formed by an equally sharp ridge formed by the basioccipital confluent with that of the basisphenoid. Medially to the deep rim of the *fenestra ovalis* the under surface of the basisphenoid and basioccipital appears as a wide deep groove.

The strong opisthotic abutting against the basisphenoid and basioccipital forms the outer and more dorsally situated part of the border of the *fenestra ovalis.* Laterally the paroccipital bar abuts against the everted sheet of the squamosal which forms the inner face of the auditory groove.

The lower jaw, being in articulation, covers most of the quadrate in ventral view, but medially the inner rounded edge of the median condyle can be seen and laterally the posterior edge of the lateral quadratic condyle.

The sharp ventral edge of the reflected lamina of the angular is shown in fig. 6*c* as is also the unankylosed mandibular symphysis.

In occipital view (Fig. 6*d*) it is evident that the occiput is low and that the quadrate complex lies well below the *basis cranii* and that the squamosal bulging outwards lateral to the roomy temporal fossa has not carried the quadrate laterally with it. The limits of the interparietal, supraoccipital and tabulars cannot all be determined, but where uncertain are probably as shown in broken lines. The posttemporal fenestrae are large, the auditory groove fairly shallow but above the *foramen magnum* there is a very deep circular depression. The paroccipital bar is strong and the descending sheet of the squamosal covers the greater part of the face of the quadrate. The deep rims of the *fenestra ovalis* are clearly seen and are formed by the basisphenoid and basioccipital.

S.A.M. 11460. Buffelsvlei, Beaufort West. Coll. Boonstra and Marais.

This specimen consists of an imperfect anterior half of a skull smaller than that of the type. There are 5 incisors and 5 postcanines; the incisors are fairly weak, the first 4 subequal and the 5th much smaller; the postcanines

are small and slender; on both sides the 3rd is missing; they occupy 20 mm. on the left and 22 mm. on the right side; the diastema anterior to the canine as well as that posterior to it measures 12 mm. On the assumption that its smaller size and the differences in the dentition may be due to its being a juvenile I am including this specimen in the species *avidus*, but with corroborative evidence from a more fully preserved skull it may well prove to be a smaller species specifically distinct from the genotype.

S.A.M. 9012a. Klein-Koedoeskop, Beaufort West. Coll. Boonstra.

This specimen is an anterior weathered part of a snout in which the incisors agree with those of the type.

Genus *Pristerosaurus* Gen. Nov.

Fairly large Pristerognathids with the dental formula i.?, c.1, p.c.3 (in all probability there were 6 incisors); the canine small and weak; the postcanines also small and weak and closely packed; in all probability the incisors were also small and weak.

Skull fairly large (Max. Length 225? to 255? mm.); preorbital hollow shallow to very shallow without definite margins; frontal with small entry into the orbital border; postfrontal well developed; snout broader than high, not narrowed between orbit and canine; orbits in all probability in anterior half of skull. Sagittal crest of parietals high and sharp.

Pristerosaurus microdon Sp. Nov. (Fig. 7.)

Genotype. S.A.M. 9083. Rietkuil, Beaufort West. Coll. Boonstra.

A well preserved skull lacking only the precanine portion of the snout.

In lateral view (Fig. 7*a*) the maxilla is seen to be short but high. The canine is small, probably not more than 15 mm. long and antero-posterior diameter 6 mm; the three small postcanines occupy 13 mm. on the right side and 15 mm. on the left. The prefrontal is large with a rounded ridge separating a dorsal from a lateral face. The jugal is a large triradiate bone; the dorsal ramus forms the major part of the postorbital bar; the posterior ramus extends far posteriorly and with the anterior ramus of the squamosal which overlies it forms the infratemporal arch. (In this feature this early Therocephalian exhibits a condition found in the later Cynodonts and not found in the Gorgonopsians.) The anterior jugal ramus forms the infraorbital bar with its extremity wedged in between the lacrimal and maxilla.

The postorbital forms the postero-dorsal part of the orbital margin and curving towards the median line is applied to the temporal face of the sagittal crest formed by the parietal, but does not extend far in posterior direction.

The squamosal has a deep descending process supporting the quadratojugal and quadrate, but the displacement of the lower jaw has disturbed the articulatory region so that the relations here are difficult to determine.

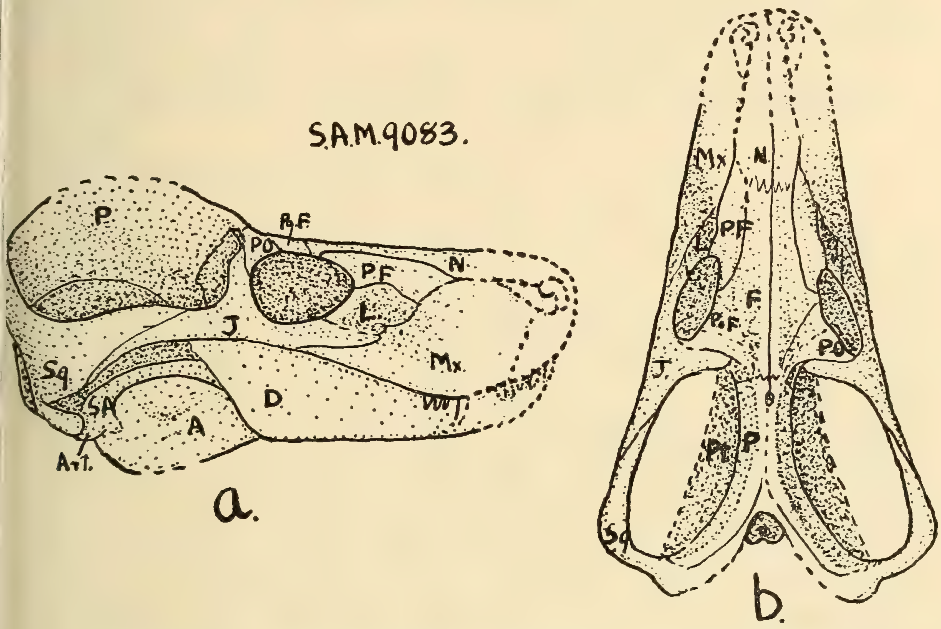


Fig. 7.—*Pristerosaurus microdon*. Type. S.A.M. 9083. ($\times \frac{1}{3}$.) *a*, Lateral view. *b*, Dorsal view. Left temporal arch corrected on basis of the right side.

The angular has a large external face with a notch situated above the reflected lamina; a curved ridge separates a dorsal hollow from the lower part of the external surface.

The temporal fossa is long and roomy.

In dorsal view (Fig. 7*b*) the high sharp parietal crest is evident. The frontal is long with a small entry into the orbital border and the prefrontal has a large dorsal face separated from the lateral face by a rounded ridge.

The occiput is deeply concave with the posttemporal arch sweeping far posteriorly. Above the *foramen magnum* the occiput is very deeply excavated; the posttemporal fossae are small; the paroccipital is strong, with its distal end everted where it meets the squamosal to form the inner boundary of the deep auditory groove.

Little of the ventral surface could be prepared; the condyle is moderately large and single; the basisphenoidal tubera are very strong (as in *Trochosaurus*) and the *fenestra ovalis* has a prominent sharp ventral rim; the parasphenoidal keel is deep and narrow. The quadrate complex is posteriorly overlapped by a sheet of the squamosal descending far ventrally.

The specimen in the British Museum B.M.N.H. R.4100 which has been referred to *Lycosuchus* and then to *Scymnosaurus* can obviously not be included in either of these two genera and undoubtedly falls within the limits set for the genus instituted here and constitutes a second species — *Pristerosaurus watsoni* (Broom).

Measurements. *Glanosuchus, Ptomalestes* and *Pristerosaurus*

	Glanosuchus.				*Ptomalestes.*		*Pristerosaurus.*
	637	11843	11964	903	11942	11460	9083
Pr.Mx.—B.O. condyle	310	300?	—	—	250	—	210?
Pr.Mx—Post.Sq. edge	321?	315?	—	—	258	—	234?
Pr.Mx.—Ant.Orb. border	172	169	—	—	132	115?	90?
Pr.Mx.—Pin.For.	235	233	—	—	185	—	153?
Width of Snout over Canines	82	80	70	—	65	70	48?
Width of Snout over last P.C.	85	85?	71	—	95	75	58
Width Interorbital	52	54	—	—	44	—	40
Width Intertemporal over Pin.For.	25	23	—	—	24	—	20
Height of Snout at Post. Edge of Canine	80	61	—	86	55	47	55?
Height at P.O. bar	53	55?	—	—	40?	—	45
Length of Upper Incisor Series l.	55	47	45	—	40	35	—
r.	55	50	45	45	40	35	—
Diastema C.—I. l.	—	10	17	—	13	12	—
r.	7	13	16	10	15	13	—
Diastema C.—P.C. l.	—	—	—	—	12	12	2
r.	16	18	15	12	12	12	2
Length of P.C. Series l.	—	—	—	—	—	20	16
r.	46	48?	21+	—	51	22	15
Ant.-Post.Diam. of Canine l.	20	18	18	—	13	12	—
r.	21	17	18	15	15	12	—

Genus *Therioides* Boonstra.

Boonstra, 1953, p. 58. Genotype. *T. cyniscus* Boonstra.

DIAGNOSIS

Fairly large Pristerognathids with the dental formula i.6, c.1, p.c.6; the incisors are subequal, moderately long and slender, the canine long and strong and the postcanines well spaced, small, slender teeth.

Skull fairly large (Max. Length 275 mm., as reconstructed); preorbital depression fairly deep but without abrupt margins and shallowing in the direction of the canine; frontal probably just entering orbital border; snout as broad as high, only slightly narrowed behind canines; orbit well in posterior half of skull.

Mandibular symphysis fairly weak, but mentum fairly upright.

Quadrate situated very low down in skull, far ventral of the occipital condyle.

Therioides cyniscus Boonstra. (Fig. 8.)

Boonstra, 1953, p. 58. Holotype. S.A.M. 11888. Vindraersfontein, Beaufort West. Coll. Boonstra.

A slightly distorted and somewhat weathered skull, together with part of the pectoral girdle, humerus, radius, ulna and part of manus.

In lateral view (Fig. 8) the maxilla is seen to be fairly low but long with a moderate overlap on the premaxilla; the small and slender postcanines are evenly spaced, occupying 39 mm. on the left and 40 mm. on the right side with a diastema of 10 mm. on the left and 9 mm. on the right side to the canine; the canine is robust and 48 mm. long; no "step" anterior to canine, and the diastema to the last incisor is small (10 mm. on left and 9 mm. on right). On the premaxilla there are 6 incisors occupying 33 mm. on the right and 5 incisors occupying 30 mm. on the left side; they are slender with a mean length of 15 mm.; the 6th is weaker than the anterior teeth. All the teeth have serrated sharp posterior edges. The septomaxilla has a fairly large facial exposure and the septomaxillary foramen is large.

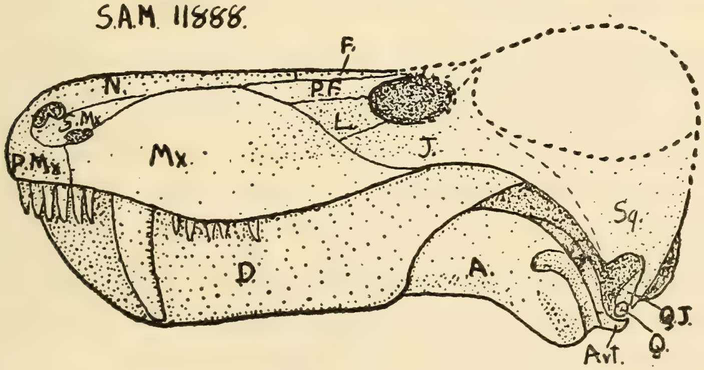


FIG. 8.—*Therioides cyniscus*. Type. S.A.M. 11888. (× ⅓.)
Lateral view. Incorporating features of the right side.

The prefrontal is fairly large with a dorsal and a smaller lateral face. The jugal bar is strong. The squamosal has a very deep descending process

carrying the quadrate very far down in the skull with the result that the articulation is situated on the same level as the ventral border of the dentary. I have recently described this area in detail (Boonstra, 1953).

The occiput is only partly preserved. The paroccipital is strong and its ventro-median corner well developed and this, together with the basioccipital and basisphenoid processes, forms the strong rim of the *fenestra ovalis,* which is thus situated low down in the skull, well below the level of the occipital condyle. The basisphenoidal tubera are well developed and the parasphenoidal keel deep. The posttemporal fenestra is fairly large and the auditory groove well developed. The lateral sweep of the squamosals has not carried the quadrates far laterally.

Genus *Pristerognathus* Seeley.

Seeley, 1895, p. 994. Genotype. *P. polyodon* Seeley.

DIAGNOSIS

Pristerognathids with the dental formula i.$\frac{6}{3}$, c.1, p.c.$\frac{3?}{3}$.

Pristerognathus polyodon, Seeley.

The holotype is in the British Museum (Natural History), B.M.N.H. R. 2581, Tamboerfontein, Beaufort West, and consists of a poor weathered snout.

This genus has only historical importance since the poor genotype shows only the following diagnostic characters: dental formula, i.$\frac{6}{3}$, c.1, p.c.$\frac{3?}{?}$. In the premaxilla the first incisor's root has a circular cross section and it lies close to its fellow; incisors 2-5 are ovate in section and the 6th is smaller than the anterior teeth; they occupy 35 mm. In the dentary there are three incisors decreasing in size in posterior direction; they are long and curved with finely serrated posterior edges; they occupy 17 mm. The upper canine has a diameter of 14 mm. and a serrated posterior edge. There is a step in the maxillary border anterior to the canine. The symphysis, formed chiefly if not entirely by the dentary, is unankylosed and the mentum is sloping. The width of the snout is 55 mm. and the height 46 mm. The bulge of the maxilla above the canine has a sub-crocodilian pitted surface.

Pristerognathus baini (Broom).

Broom, 1904, p. 87. Holotype. S.A.M. 583. Locality unknown. Coll. unknown.

A very poor weathered snout fragment.

There are roots of 6 upper and 3 lower incisors. The upper incisors occupy 34 mm. (measured round the curve); the 6th is smaller than the preceeding teeth; the first smaller than the succeeding 3 and lies close to its fellow. There is no reason for this fragment to bear a distinct specific name and I regard *baini* as a synonym of *polyodon*.

I propose that the generic name *Pristerognathus* be retained for Seeley's historic specimen and be used as a suitable label for all Pristerognathid Therocephalian specimens in which no other diagnostic characters are shown except the presence of 6 upper incisors occupying a space of 35 mm. For specimens showing other additional characters other generic names should be used as has already been done viz. *Alopecognathus, Cynariognathus,* etc.

The following list of specimens comprises a number of fragmentary and weathered snouts which on the nature of the incisors can only be referred to the genus *Pristerognathus* as characterised above.

S.A.M.	631	Koup. Coll. Joubert.
,,	751	Seekoeigat, P.A. Coll. Du Plessis.
,,	752	Seekoeigat, P.A. Coll. Du Plessis.
,,	1075	Rietfontein, P.A. Coll. J. H. Whaits.
,,	1213	Unknown locality.
,,	3432	Janwillemsfontein, P.A. Coll. Haughton & Whaits.
,,	9015	Klein-Koedoeskop, B.W. Coll. Boonstra.
,,	9084a	Rietkuil, B.W. Coll. Boonstra.
,,	9111	Die Vlei, P.A. Coll. Boonstra.
,,	11456	Buffelsvlei, B.W. Coll. Boonstra & Marais.
,,	11586	Koedoeskop, B.W. Coll. Boonstra.
,,	11842	Lammerkraal, P.A. Coll. Boonstra.
,,	11848	Veldmansrivier, P.A. Coll. Boonstra.
,,	11871	Perdewater, P.A. Coll. Boonstra.
,,	11872	,, ,, ,, ,,
,,	11873	,, ,, ,, ,,
,,	11874	,, ,, ,, ,,
,,	11875	,, ,, ,, ,,
,,	11876	,, ,, ,, ,,
,,	11936	Bosluiskraal, Laingsburg. Coll. Boonstra.
,,	11956	Klein-Koedoeskop, B.W. Coll. Boonstra.
,,	11957	Abrahamskraal, P.A. Coll. Le Roux.
,,	11960	Dikbome, Laingsburg. Coll. Boonstra.
,,	11963	Dikbome, Laingsburg. Coll. Boonstra.
,,	11965	Skoppelmaaikraal, Laingsburg. Coll. Botes.
,,	11966	Seekoeigat, P.A. Coll. T. Bain.
,,	11967	Seekoeigat, P.A. Coll. T. Bain.

Genus *Alopecognathus* Broom.

Broom, 1915, p. 116. Genotype. *A. angusticeps* Broom.

The holotype of this species is in the American Museum of Natural History. A.M.N.H.5559. Coll. Whaits.

DIAGNOSIS

Moderate to fairly large Pristerognathids with the dental formula i.6, c.1, p.c.4-5; the anterior incisors are fairly long, slender teeth (the 1st incisors, as in all Pristerognathids, are smaller than the 2nd to 5th) but the 6th is appreciably to very much smaller; the canine is long and strong; the postcanines are small and fairly weak, not close set.

Skull moderate to fairly large (Max. Length 240? mm. to 276 mm.); preorbital hollow varies from a fairly shallow hollow shallowing evenly in the direction of the canines and without abrupt borders to a deep depression with sharply demarcated borders especially anteriorly; septomaxilla with well developed facial exposure and septomaxillary foramen well developed; frontal with small entry into orbital border or just excluded from it; prefrontal large with well marked dorsal and lateral face; postfrontal moderately to well developed; snout wider than high, broader over last postcanines than over canines; orbits just entering anterior half of skull.

Mandibular symphysis weak and mentum sloping very much.

Sagittal crest of parietals moderately high but with sharp edge.

Quadrate low down, but well above the level of the lower border of the dentary.

Temporal fossa fairly long and wide.

Squamosal with everted lateral edge.

Alopecognathus angusticeps Broom.

The holotype in the American Museum has been redescribed by me some years ago when studying the South African specimens sold by Dr. Broom to the American Museum (Boonstra, 1935; p. 2).

DIAGNOSIS

There are 5-6 postcanines; maximum length of skull 275 mm.; preorbital depression fairly shallow to deep, extending in direction of canine; postfrontal well developed; squamosal laterally everted.

S.A.M. 9112 (Fig. 9). Stinkfontein, Prince Albert. Coll. Boonstra.

A fairly well preserved anterior three quarters of a skull.

From the figures and from the accompanying list of measurements it is clear that this specimen from Stinkfontein is co-specific with the genotype,

notwithstanding certain less important differences e.g. in our specimen there are 6 postcanines occupying 40 mm., and the preorbital depression is deep.

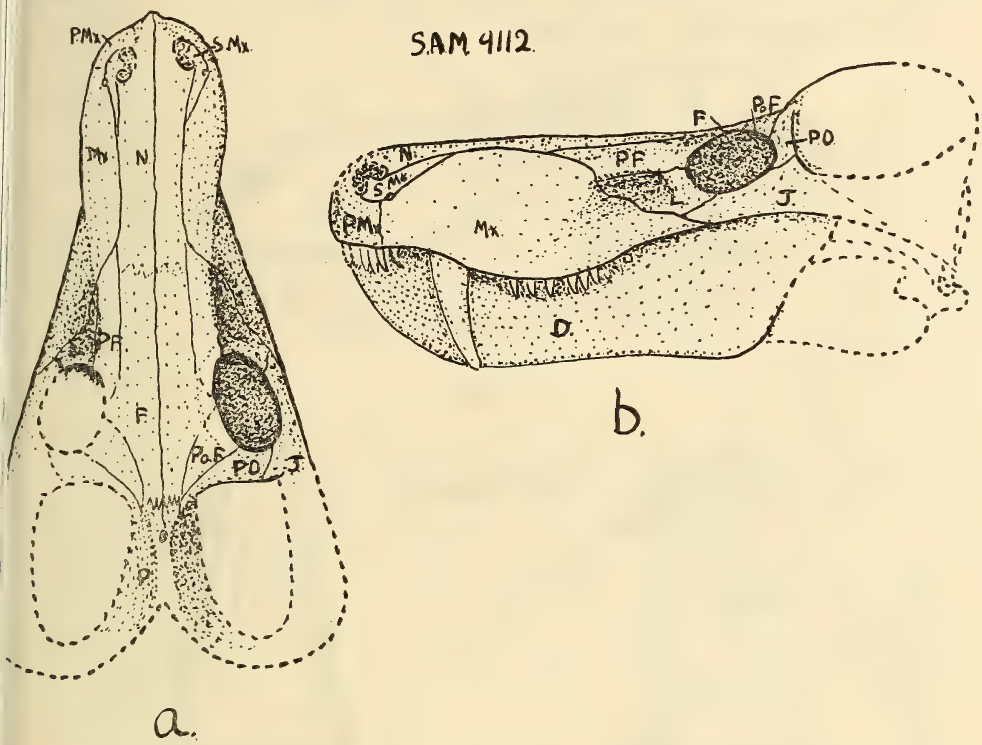


FIG. 9.—*Alopecognathus angusticeps.* S.A.M. 9112. (× ⅓.)
a, Dorsal view. *b,* Lateral view.

This specimen allows us to correct two points in my description (Boonstra, 1935) of the genotype viz. with the anterior part of the sagittal crest preserved it is now clear that in my reconstruction the height of the crest should have been much higher; the preserved frontonasal suture in this specimen shows that the broken line indication in my figure of 1935 should have been further forward so that the frontal is a long narrow bone and the nasal shorter than I thought in 1935.

Alopecognathus angustioriceps (Boonstra).

Boonstra, 1953, p. 63. Holotype. S.A.M. 9342. (Fig. 10.) Kroonplaas, Beaufort West. Coll. Boonstra.

A very good undistorted and practically complete skull.

Diagnosis

There are 5 postcanines; maximum length of skull 252 mm.; preorbital depression shallow, continued anteriorly as a shallow groove; postfrontal small; squamosal with lateral bulge.

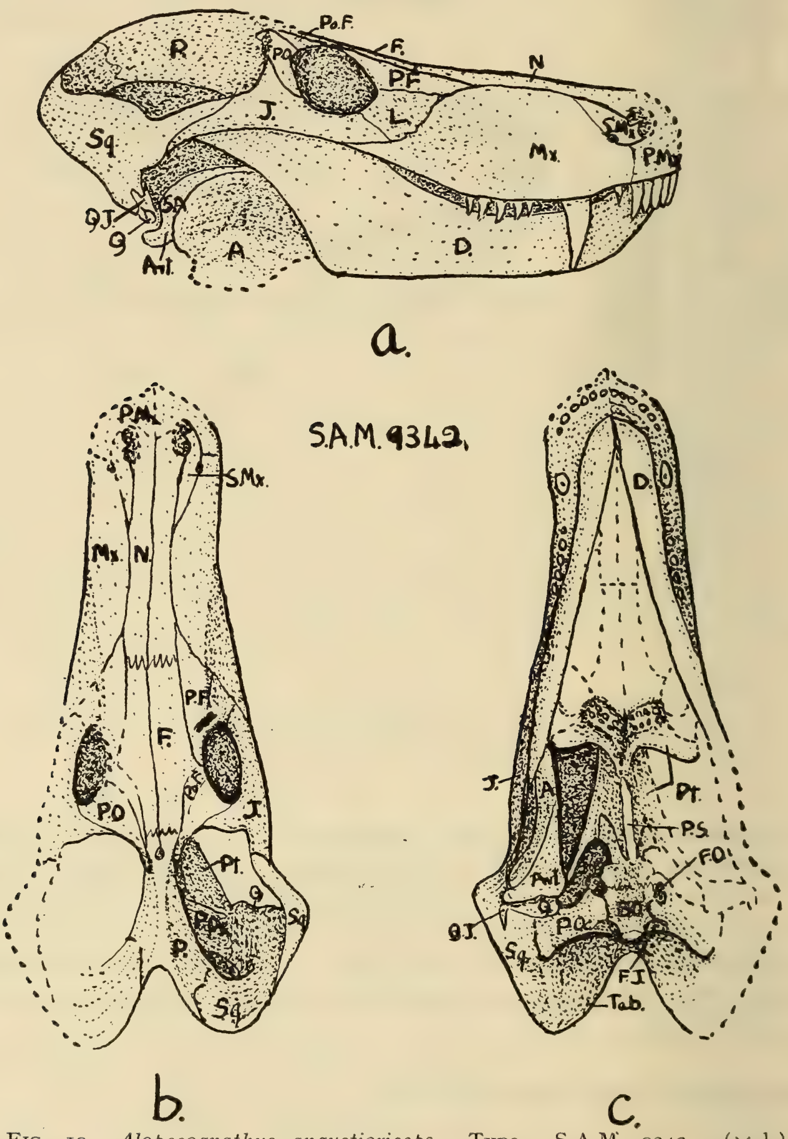


Fig. 10.—*Alopecognathus angustioriceps*. Type. S.A.M. 9342. (× ⅓.)
a, Lateral view. *b*, Dorsal view. *c*, Ventral view.

In lateral view (Fig. 10*a*) the maxilla is seen to be fairly low and of moderate length with a moderate overlap on the premaxilla; it carries 5 small

(1st very small) postcanines occupying 27 mm. on the left and 29 mm. on the right side. The diastema between canine and the first postcanine is 10 mm. on the left and 11 mm. on the right. The canine is well developed with a length of 30? mm. and antero-posterior diameter of 14 mm. Anterior to the canine is a diastema of 12 mm. on the left and 14 mm. on the right. The premaxilla carries 6 teeth, the anterior 5 are long and slender and the 6th small and slender occupying 33 mm. on both sides.

The septomaxilla has a well developed facial surface and intra-nostril spur. The prefrontal has a small lateral face. The jugal has a short dorsal ramus and a well developed posterior ramus overlain by a moderately long anterior ramus of the squamosal. The postorbital forms most of the postorbital bar. The squamosal has a deep descending ramus supporting the quadrate complex. I have recently figured and described the suspensorial region (Boonstra, 1953). The dentary is large with a strong coronoid process; the symphysis is weak and the mentum sloping.

In dorsal view (Fig. 10*b*) the long slender shape of the skull is evident; the orbits just enter the anterior half of the skull; the temporal fossa is long and roomy; the everted anterior ramus of the squamosal forming most of the lower temporal arch is noteworthy (seen also in the genotype). The frontal is just excluded from the orbital margin; both the frontal and nasal are narrow. The prefrontal has a large dorsal face bounded laterally by a sharp ridge. The postfrontal is small and the postorbital well developed but extending little along the lateral face of the parietal. The parietals are narrow and form a sharp sagittal crest which is, however, not high. The upper occipital edge is very deeply concave.

In ventral view (Fig. 10*c*) it is seen that with the dentaries in position it has not been found feasible to clean the anterior part of the palate. Just anterior to the transverse rami of the pterygoids the pterygoids bear two dentigerous ridges. The lateral corner of the transverse pterygoidal ramus lies in the plane of the angle of the dentary but does not descend to the level of the ventral edge of the dentary. Posteriorly the pterygoid clasps the parasphenoidal rostrum which lies in the median line and the quadrate ramus, with a slightly curved lateral edge, extends to the quadrate. The parasphenoidal keel is deep. The basisphenoidal tuber, the medio-ventral corner of the opisthotic and the antero-lateral corner of the basioccipital form three distinct protuberances which constitute the tripartite rim bounding the *fenestra ovalis*. The paroccipital bar is strong; the basioccipital condyle fairly weak. The squamosal extends down far to cover the posterior face of the quadrate complex. The squamosal sweeps far posteriorly to make the occiput deeply concave, and the occipital condyle and the quadratic condyles are situated far anterior to the posterior limits of the skull. The quadratic condyles also lie in a plane well ventral to that of the occipital condyle.

Measurements. *Alopecognathus*

		A.M.N.H. 5559	S.A.M. 9112	S.A.M. 9342
Pr.Mx.—B.O. condyle		234	—	215
Pr.Mx.—Post.Sq. edge		275	260	252
Pr.Mx.—Ant.Orb. border		140	138	117
Pr.Mx.—Pin.For.		210	210	180
Width of Snout over Canines		55	56	50
Width of Snout over last P.C.		68	70	53
Width Interorbital		35	45	40
Width Intertemporal over Pin.For.		10?	15	17
Height of Snout at Post. edge of Canine		50	51	48
Height at Post.Orb. bar		45	42	45
Length of Upper Incisor Series	l.	33	34?	33
	r.	—	34?	33
Diastema C.—I.	l.	12	12	12
	r.	—	—	14
Diastema C.—P.C.	l.	12	16	10
	r.	—	—	11
Length of P.C. Series	l.	31	40	27
	r.	—	39	29
Ant.-Post.Diam. of Canine	l.	12	15	13
	r.	—	—	13

Genus *Cynariognathus* Broom.

Broom, 1931, p. 161. Genotype. *C. platyrhinus* Broom.

The holotype of this species is in the American Museum of Natural History. A.M.N.H. 5502. Collected by J. H. Whaits and sold to the American Museum by Dr. Broom.

Diagnosis

Medium sized Pristerognathids with the dental formula i.5-6, c.1, p.c.6-9; the posterior incisors are smaller than the anterior ones; the canine is long and strong; the postcanines are fairly strong and closely set.

Skull of medium size (Max. Length 260-290 mm.); preorbital depression shallow; septomaxilla fairly small; frontal with a moderate entry into the orbital border; prefrontal large with well marked dorsal and lateral face; postfrontal moderately developed; snout broader than high; broader over last postcanines than over canines; orbit in posterior half of skull; skull low over postorbital bar; orbits high up in the skull. Premaxilla weak. Angle

of dentary obtuse with posterior edge of dentary not deeply concave. Dentary not shallow behind the canine.

Cynariognathus paucioridens. Sp. Nov. (Fig. 11.)

Holotype. S.A.M. 11560a. Kroonplaas, Beaufort West. Coll. Boonstra.

A weathered snout with some parts of the postcranial skeleton.

DIAGNOSIS

Six closely packed postcanines occupying 27 mm. on the left and 28 mm. on the right side; breadth of snout over the canines 50 mm.; height of snout at posterior edge of canine 40 mm.; preorbital length of skull 99 mm.

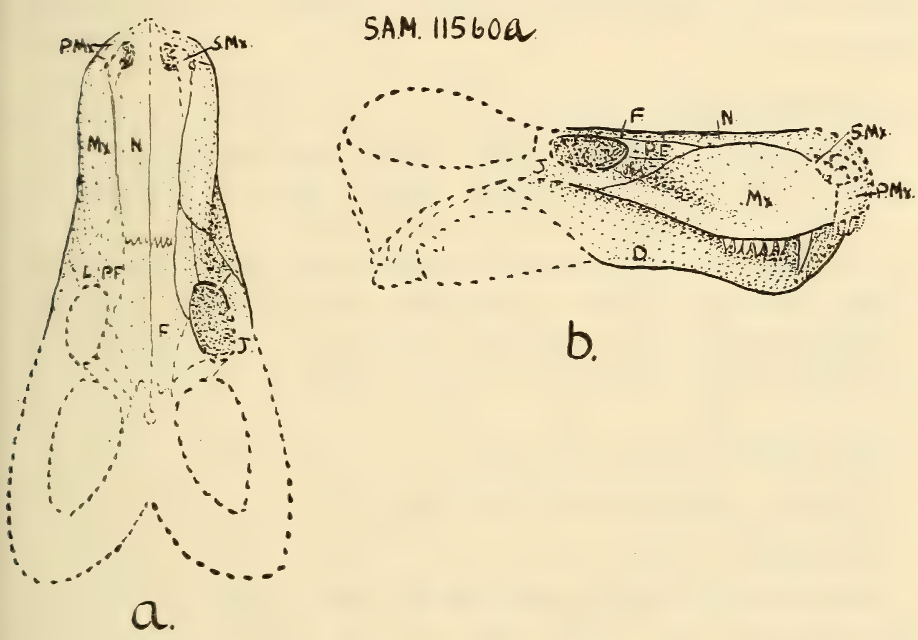


FIG. 11.—*Cynariognathus paucioridens.* Type. S.A.M. 11560a. (× ⅓.)
a, Dorsal view. *b*, Lateral view.

This skull has a long low maxilla, the lacrimal is large and the prefrontal fairly small; the dentary is fairly lightly built; the preorbital groove is fairly deep. Little more can be determined from this specimen and I would have hesitated to name it were it not that a second specimen, also with 6 closely packed postcanines, proves that we have here a definitely new species of *Cynariognathus*.

S.A.M. 11586. Koedoeskop, Beaufort West. Coll. Boonstra.

The antorbital weathered half of a skull.

Here there are 6 closely packed, fairly weak postcanines occupying 28 mm. and there are apparently 5 incisors occupying 30 mm.; the height of the snout is 40 mm. and the width 53 mm.; the antorbital length is 100? mm.

S.A.M. 1080. Fraserburg Rd., Prince Albert. Coll. J. H. Whaits.

A weathered antorbital part of a skull together with a complete hindfoot.

In this specimen there are 7 postcanines; they are closely set and robust and occupy 26 mm. The height of the snout is 35 mm. and its breadth 48 mm.; the antorbital length as estimated is only 75 mm. The shorter snout and the larger number of postcanines make inclusion in the above species provisional.

Cynariognathus spp.

S.A.M. 3713. Bloukrans, Prince Albert. Coll. Haughton.
S.A.M. 9088a. Klein-Koedoeskop, Beaufort West. Coll. Boonstra.
S.A.M. 11968. Locality and Collector unknown.

These three incomplete snouts are included in the genus *Cynariognathus* as the height of the snouts is much smaller than the breadth and because in the postcanine series the teeth are closely packed. But as the posterior postcanines are not preserved the determination of the species remains uncertain.

Genus *Pristerognathoides* Gen. Nov.

Genotype. *Alopecognathus minor* Haughton.

Diagnosis

Medium sized Pristerognathids with the dental formula i.6, c.1, p.c.5-6; the incisors are small to fairly strong teeth, with the 6th incisor only slightly to much smaller than its predecessors; the canine is fairly long; the postcanines are small, weak and well spaced.

Skull of medium size (Max. Length 222-287 mm.); preorbital depression shallow to fairly shallow continuing as a groove in the direction of the canine; septomaxilla fairly small; frontals with a fairly small entry into the orbital border; prefrontal large with well marked dorsal and lateral face; postfrontal moderately well developed; snout wider than high; broader over last postcanine than over canines; orbits in posterior half of skull or just entering anterior half; skull very low over postorbital bar; orbits high up in skull.

Sagittal crest high and with sharp edge. Quadrate fairly low down, but well above the level of the lower border of the dentary.

Temporal fossa fairly long and moderately wide.

Premaxilla weak.

Squamosal with lateral edge not everted.

Angle of dentary squarish with fairly deep concave posterior edge sweeping far posteriorly towards the coronoid process. Dentary shallow behind lower canine.

Pristerognathoides minor (Haughton). (Fig. 12.)

Haughton, 1918, p. 180. Holotpye. S.A.M. 3415. Klipbank, Beaufort West. Coll. Whaits.

A good skull lacking only the temporal arches.

DIAGNOSIS

There are 4 postcanines; maximum length of skull 240? mm.; preorbital depression deep with very definite and abrupt margins; postfrontal large.

Since Haughton's description I have carried the development of the skull further, exposing more of the palate, and removed the matrix from the preorbital depression.

In lateral view (Fig. 12*a*) the maxilla is seen to be low and long with a long overlap on the premaxilla; on the right 4 postcanines are preserved but there is a space between the 1st and 2nd which may have housed an additional tooth; the length of the series is 28 mm.; on the left 3 postcanines are preserved with a gap between the 1st and 2nd; the length of the series is 26 mm.; the postcanines are short but stout. Between the 1st postcanine and the canine there is a diastema of 8 mm. on the left and 12 mm. on the right side. The canine is long and strong (diameter 11-12 and length 24? mm.). Anterior to the canine there is a diastema of 10 mm. to the last incisor. There are 6 incisors of which the 5th and 6th are shorter than the anterior ones and the series occupies 32 mm. on both sides. All the teeth have finely serrated posterior borders.

The septomaxilla has a fairly large facial exposure and a well developed intra-nostril spur; the septomaxillary foramen is fairly large. The preorbital depression is a deep hollow, especially on the right side, with a sharp rim, especially along its dorsal and ventral borders; a low longitudinal ridge divides the hollow into two equal parts on the right side, but on the left the lower part is the larger; anteriorly the hollow ends abruptly and is not continued in the direction of the canine.

The bulge of the maxilla above the canine is not rugosely pitted. The anterior orbital border just enters the anterior half of the skull. The

postfrontal is very well developed with a large entry into the orbital border; whereas the postorbital appears to have only a very small entry into the orbital border, forming the posterior part of the postorbital bar.

The edge of the sagittal crest is not preserved but was probably sharp and fairly high with little flanking of the parietal by the postorbital.

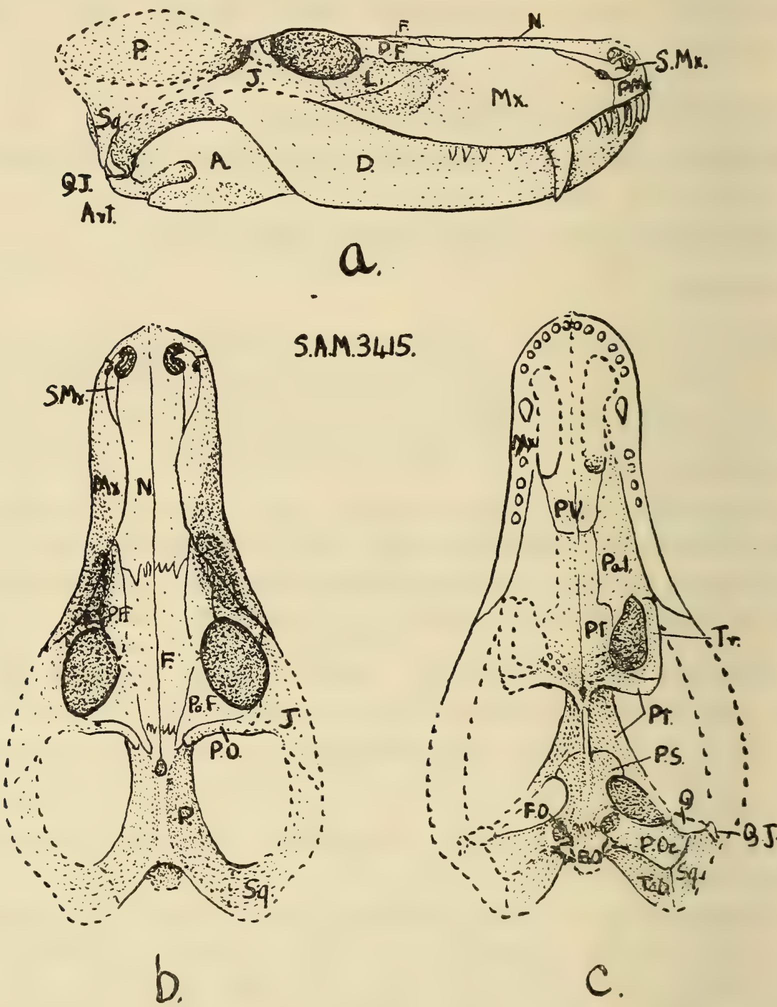


FIG. 12.—*Pristerognathoides minor.* Type. S.A.M. 3415. (× ½.) *a,* Lateral view. Incorporating features of the left side. *b,* Dorsal view. *c,* Ventral view.

The articulatory region is not well shown since the bone has been stripped. The angular has a deep notch and a small bone above the articular I have

identified as the quadratojugal. The squamosal has a deep descending process posteriorly supporting the quadrate complex.

In dorsal view (Fig. 12*b*) the width across the temporal arches (as restored) is great making a roomy although short temporal fossa, whereas the snout, unconstricted behind the canines, is relatively narrow. The frontal is fairly small and probably just excluded from the orbital border. The postfrontal is very large and the postorbital weak, both with little posterior prolongation along the lateral face of the parietals. The prefrontal has a well developed dorsal face separated from the smaller lateral face by a sharp ridge which also forms the sharp dorsal rim of the preorbital depression. The nasals are large, expanded anteriorly and posteriorly. The dorsal occipital edge is deeply concave.

In ventral view (Fig. 12*c*) development has exposed all but the choanal region of the palate. The posterior ends of the prevomers form a shovel-shaped sheet of bone underlying the palatines and pterygoids. The pterygoids have long anterior rami, which bear, in their posterior part, a dentigerous ridge; the transverse pterygoidal ramus is not very strong or wide and its anterior face is lined by a descending sheet of the transversum which extends anteriorly as a girderlike ramus to form the outer border of the large suborbital vacuity. There is a small interpterygoid vacuity. The outer edge of the quadrate ramus of the pterygoid is slightly concave, thus increasing the size of the temporal space. In the median line the parasphenoid underlies the basisphenoid and anteriorly forms a deep keel. Surrounding the *fenestra ovalis* there is a fairly strong rim formed by the basioccipital, opisthotic and basisphenoid-parasphenoid. The paroccipital bar is strong and its ventro-anterior corner abuts against the quadrate. Lateral to the quadrate lies a small quadratojugal which does not enter the condylar surface. The squamosal covers most of the posterior face of the quadrate complex.

S.A.M. 4332 (Fig. 13.) Wilgerbos, Prince Albert. Coll. Haughton.

A good skull of which some aspects of the internal structure have been described by Haughton (Haughton, 1918).

The skull is very similar to that of the holotype of *Pristerognathoides minor*. On the left side there are 5 postcanines occupying 29 mm. The distance between canine and postcanines is 15 mm. on the left side and between canine and postcanines is 15 mm. on the left side and between canine and incisor the diastema is 9 mm. and the 6 incisors measure 30 mm.

The preorbital depression is fairly deep, but shallows in the direction of the canine.

As is evident from the figures there are several other minor differences in the proportions of some of the surface bones, but notwithstanding these I am referring this skull to *P. minor*.

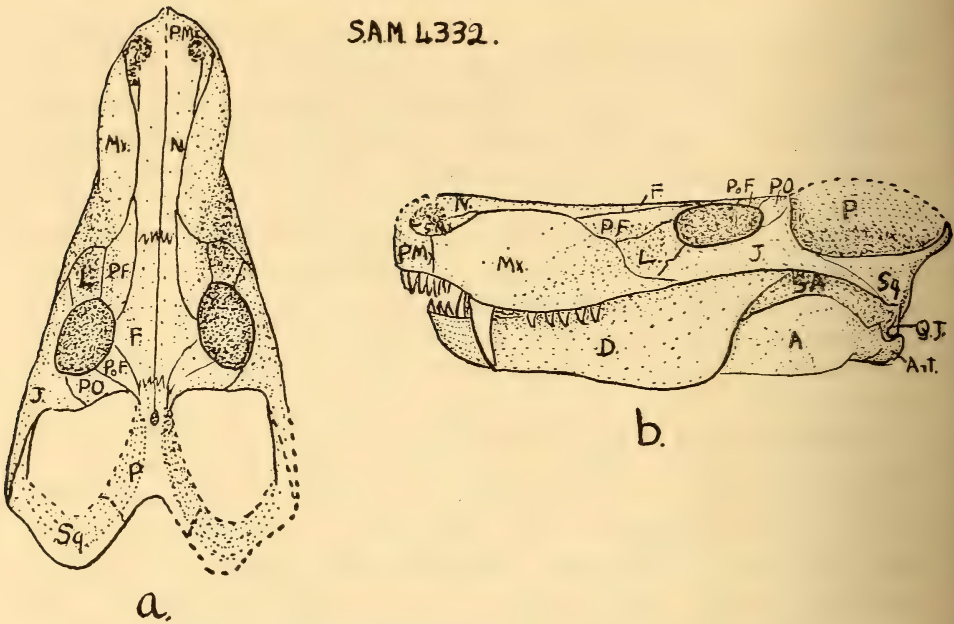


FIG. 13.—*Pristerognathoides minor*. S.A.M. 4332. (× ⅓.)
a, Dorsal view. *b*, Lateral view.

S.A.M. 3435 (Fig. 14). Jakkalsfontein, Prince Albert. Coll. Rogers. A well preserved antorbital part of a skull laterally compressed.

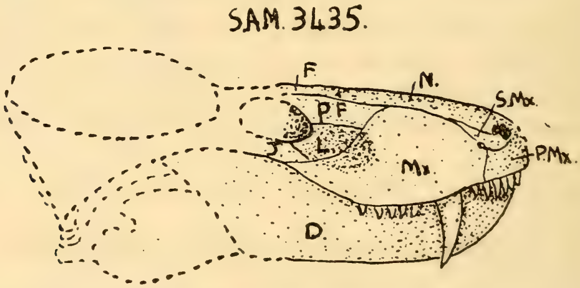


FIG. 14.—*Pristerognathoides minor*. S.A.M. 3435.
(× ⅓.) Lateral view.

Although the snout as preserved appears to be shorter and the maxilla consequently relatively higher and shorter than in the type, the dentition is very similar and the clearly demarcated preorbital depression has an abrupt anterior border as in the type specimen. I am thus referring this snout to *P. minor*.

S.A.M. 11891 (Fig. 15). Lammerkraal, Prince Albert. Coll. Boonstra & Pienaar.

A good skull lacking only the right postorbital and temporal arches.

In this skull there are on the right side roots of six postcanines. The snout is broader than in the type and the preorbital depression is fairly shallow and although there are other minor differences as can be seen from the figures and the table of measurements I am referring it to the species *minor*.

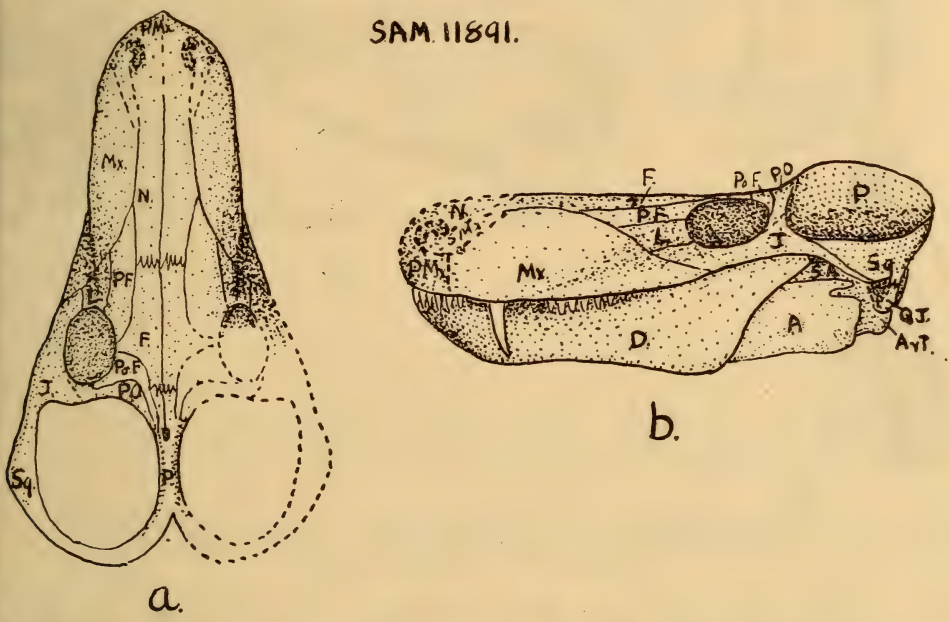


FIG. 15.—*Pristerognathoides minor*. S.A.M. 11891. (× ⅓.)
a, Dorsal view. *b*, Lateral view.

Pristerognathoides roggeveldensis (Boonstra). (Fig. 16.)

Boonstra, 1953, p. 60. Holotype. S.A.M. 9356a. Roggekloof, Sutherland. Coll. Walker.

A fair though somewhat distorted skull lacking the posterior part of the skull roof.

DIAGNOSIS

Skull long and narrow; with five weak, well spaced postcanines; incisors fairly strong with the 6th only slightly smaller than the 5th; orbit well in posterior half of skull; squamosal extending well forward on lateral face of parietal; prefrontal narrow.

In lateral view (Fig. 16*b*) the maxilla is seen to be long and high; the septomaxilla has a moderate facial exposure; the orbit is small and situated high up in the skull; the lacrimal large and the preorbital depression fairly shallow. I have recently (Boonstra, 1953) described the articulatory region.

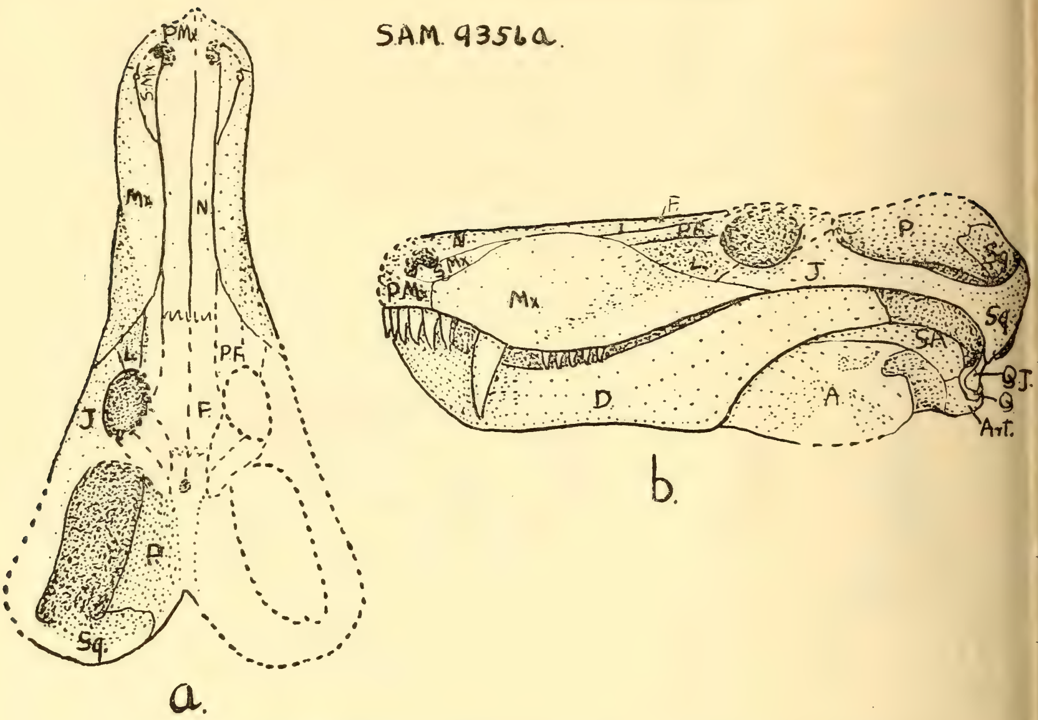


Fig. 16.—*Pristerognathoides roggeveldensis*. Type. S.A.M. 9356a. (× ⅓.) *a*, Dorsal view. *b*, Lateral view.

In dorsal view (Fig. 16*a*) the snout appears long and narrow and the temporal fossa long and narrow.

Pristerognathoides vanwyki (Broom). (Fig. 17.)

Broom, 1925, p. 318. Holotype. S.A.M. 6533. Bloukrans, Prince Albert. Coll. Le Roux.

A weathered and distorted skull.

Diagnosis

Skull moderately long and narrow; with six weak well spaced postcanines; incisors fairly weak, with the sixth very slender; orbit just in posterior half of skull; prefrontal large.

In lateral view (Fig. 17*b*) the maxilla is seen to be fairly short and high; the septomaxilla has a good facial exposure; the orbit is small and situated high up in the skull; the lacrimal is large and the preorbital depression shallow.

In dorsal view (Fig. 17*a*) the skull is fairly long and fairly narrow and the temporal fossa fairly short and narrow.

S.A.M. 11893 (Fig. 18). Lammerkraal, Prince Albert. Coll. Pienaar.

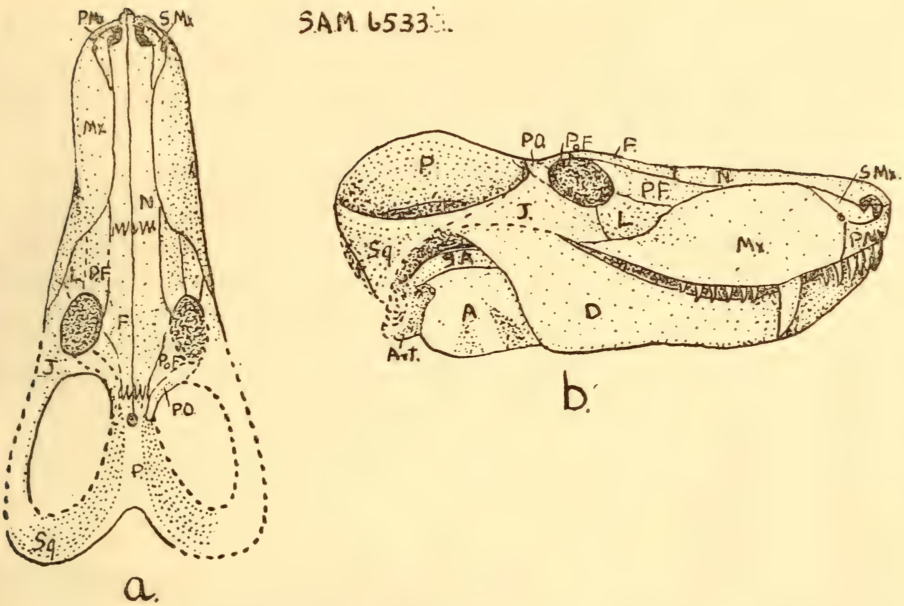


FIG. 17.—*Pristerognathoides vanwyki*. Type. S.A.M. 6533. ($\times \frac{1}{3}$.)
a, Dorsal view. *b*, Lateral view. Incorporating features of the left side.

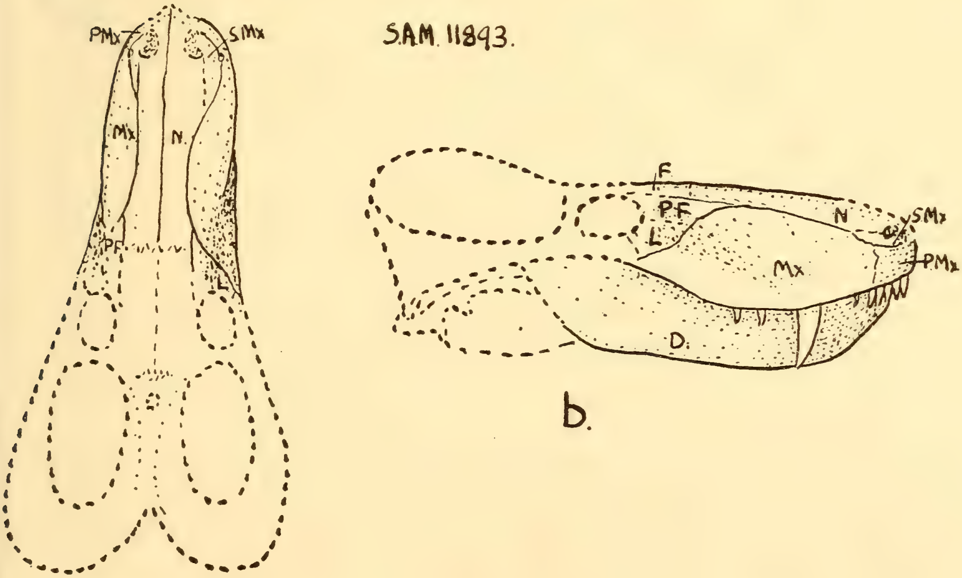
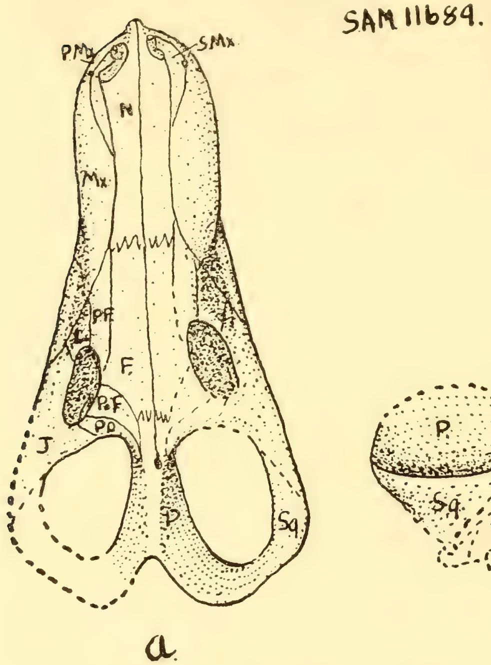


FIG. 18.—*Pristerognathoides vanwyki*. S.A.M. 11893. ($\times \frac{1}{3}$.)
a, Dorsal view. *b*, Lateral view.

This snout, presented to the Museum by Mr. J. Pienaar of Lammerkraal, has only two postcanines preserved, but as this is probably only due to postmortem loss and the other characters preserved agree fairly well with those of *vanwyki* I am referring it to that species.

S.A.M. 11689 (Fig. 19). Prince Albert Road. Coll. Hesse.



This dorso-ventrally crushed skull has the postcanines badly preserved but there were probably 6. Although the snout is longer and there are differences of actual size and proportions I am referring it to *vanwyki*.

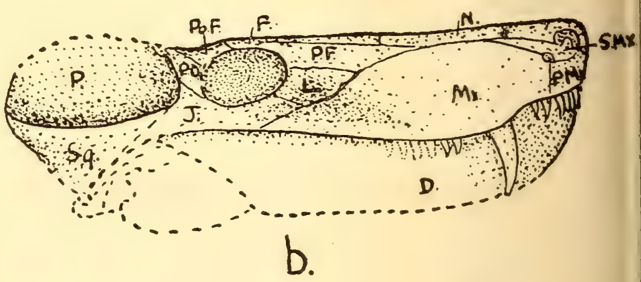


FIG. 19.—*Pristerognathoides vanwyki*. S.A.M. 11689. (× ⅓.) *a*, Dorsal view. *b*, Lateral view. Dorso-ventral crushing corrected.

Pristerognathoides parvus Sp. Nov. (Fig. 20.)

Holotype. S.A.M. 3611. Bloukrans, Prince Albert. Coll. Scholtz. A weathered anterior two thirds of the skull.

Diagnosis

Small low and fairly narrow skull; with 5 small well spaced postcanines; incisors weak with the 5th weaker than the anterior ones and the 6th very feeble, the diastema between incisors and canine great (15 mm.), and canine slender; prefrontal large; very low over postorbital arch.

The skull is small with the maximum length probably not more than 195 mm., the maxilla is long and low; the suborbital arch slender and the dentary weak; the preorbital depression quite deep.

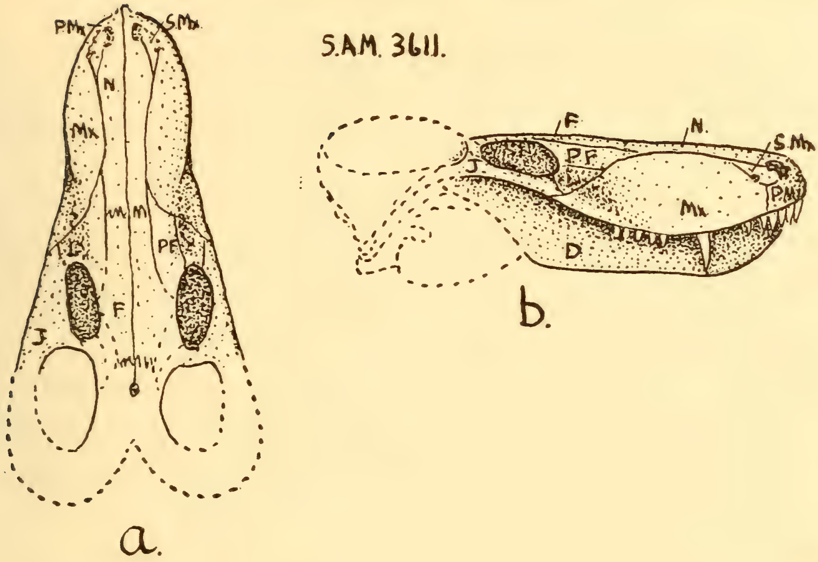


FIG. 20.—*Pristerognathoides parvus* Sp. Nov. Type. S.A.M. 3611. (× ⅓.) *a,* Dorsal view. *b,* Lateral view. Incorporating some features of the left side.

MEASUREMENTS—*Pristerognathoides*

		3415	4332	3435	11891	9356a	6533	11893	11689	3611
Pr. Mx.—B.O. condyle		225	200	—	200	—	—	—	—	—
Pr. Mx.—Post. Sq. edge		240	218	—	215	255	222?	213?	235	—
Pr. Mx.—Ant. Orb. border		115	110	90	113	117	106	108?	118	97
Pr. Mx.—Pin. For.		165	155	—	160	—	158	—	177?	148
Width of Snout over Canines		50	47	—	55	52?	45	50	52	45
Width of Snout over last P.C.		55	60	—	60	—	52	57	—	59
Width Interorbital		33	35	—	30	—	25 ?	—	30	28
Width Intertemporal over Pin. For. ..		20	—	—	16	—	14	—	17	25
Height of Snout at Post. edge of Canine ..		40	45	40	39	53?	40	51	37?	40
Height at P. Orb. bar		25?	30	—	20	—	—	—	30?	30?
Length of Upper Incisor Series ..	l.	32	33	—	—	35	30?	35	30	35
	r.	32	—	30	35	—	—	34	—	35
Diastema C.—I.	l.	11	8	5	—	9	9	13	9	10
	r.	11	11	6	5	—	—	13	—	9
Diastema C.—P.C.	l.	8	15	12	15	16	10	11	12	10
	r.	11	11	9	14	10	10	10	11	8
Length of P.C. series	l.	28	30	22	26	27	27	—	—	25
	r.	29	—	27	27	25?	35	—	33?	21
Ant.-Post. Diam. of Canine	l.	12	10	10	11	12	13	12	12	5
	r.	11	10	9	7	12	12	12	11	6

Genus *Maraisaurus* Boonstra.

Boonstra, 1953, p. 62. Genotype. *M. parvus* Boonstra.

DIAGNOSIS

Small Pristerognathids with dental formula unknown but probably i.6?, c.1?, p.c.4?

Skull very small [Max. Length (as reconstructed) 162? mm.]; preorbital depression very deep with sharp rim; frontal with moderate entry into orbital border; postfrontal well developed; orbits large and just entering anterior half of skull. Sagittal crest of parietals fairly low, but with sharp edge.

Maraisaurus parvus Boonstra (Fig. 21).

Genotype. S.A.M. 11944. Buffelsvlei, Beaufort West. Coll. Marais.

The posterior two thirds of a somewhat weathered skull lacking the snout.

Lateral view (Fig. 21*b*). The articulatory region of the lower jaw has recently been figured and described (Boonstra, 1953, p. 62). The prefrontal has a sharp dorsal edge separating a small lateral from a larger dorsal face. The jugal is well developed with an anterior ramus forming the stout suborbital bar; a weaker dorsal ramus forming the lower half of the orbital bar and a fairly long posterior ramus, overlain by an anterior ramus of the squamosal, forming the anterior and much of the ventral part of the lower temporal arch. The postorbital is small forming only a small part of the orbital margin and posteriorly extending as a weak tongue on to the lateral face of the parietal.

The squamosal has a moderate descending flange carrying the quadrate complex but not extending far ventrally so that the quadratic condyle still lies well above the level of the lower border of the dentary.

In dorsal view (Fig. 21*a*) it is seen that the temporal fossa is fairly long and wide, the intertemporal region narrow and the sagittal crest low but sharp. The frontal is long and has a fairly large entry into the orbital border; the

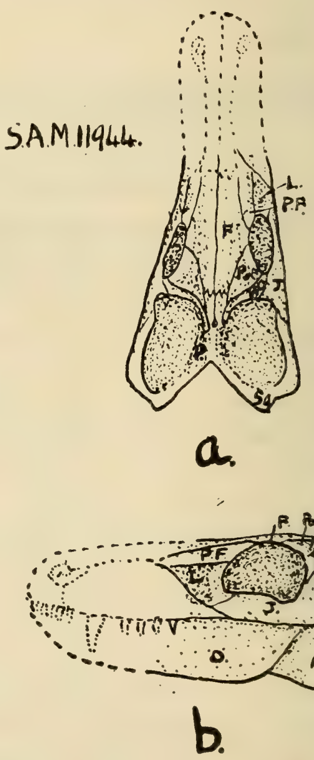


FIG. 21.—*Maraisaurus parvus*. Type. S.A.M. 11944. ($\times \frac{1}{3}$.) *a*, Dorsal view. *b*, Lateral view.

postfrontal is well developed; the postorbital has only a small entry into the orbital border and its posterior tongue weak and flanks the parietal for only a short distance; the ridge on the prefrontal sharply separates the dorsal from the lateral surface.

An Unidentified Pristerognathid.

S.A.M. 11959 (Fig. 22). Dikbome, Laingsburg. Coll. Boonstra.

Fragmentary weathered skull pieces.

The dental formula is i.6, c.1, p.c.5. The incisors are robust, with the 6th strong, occupying 40 mm. on the left and 43 mm. on the right side. There is no diastema between incisors and canine and the diastema between canine and postcanines is very small (5 mm. on the right and 6 mm. on the left side). The postcanines are irregular with the first, fourth and fifth fairly weak but the third quite robust and occupying 36 mm. on the left and 45 mm. on the right side. The articulatory region has recently been described (Boonstra, 1953).

This form appears to occupy a position intermediate between genera like *Scymnosaurus* and *Cynariognathus*.

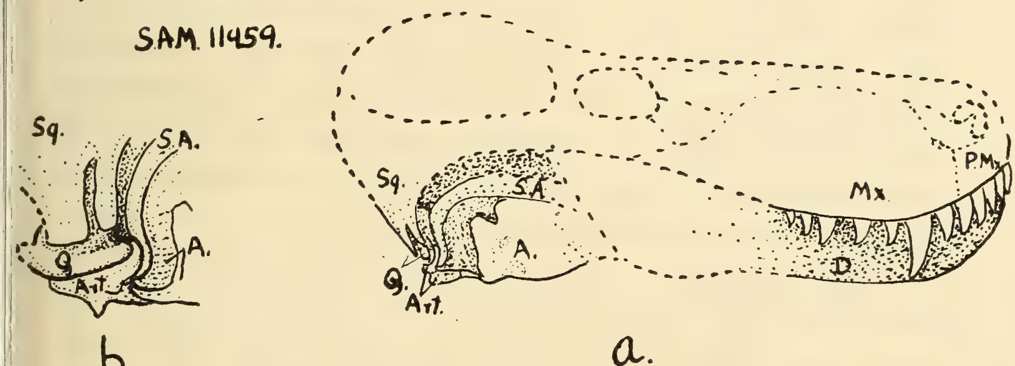


FIG. 22.—*An Unidentified Pristerognathid.* S.A.M. 11959 *a,* Lateral view (× ⅓.) *b,* Oblique view of the articular region. (× ⅔.) The quadratojugal is not preserved; when present it rested on the ledge on the posterior surface of the quadrate.

Discussion

As all recent authors derive the Therapsids from the Pelycosaurs it will be of interest to compare the Pristerognathidae — the most primitive Therocephalian family — with the Pelycosaurs. From Romer's monograph I have extracted a list of morphological features mentioned by him and am comparing the same structures as identified in the Pristerognathids.

The Pristerognathids agree with the Pelycosaurs: in most forms the frontal enters the supraorbital border, but in some this entry is small and in

some the frontal is secondarily excluded; a ridge separates a dorsal from a lateral surface in the prefrontal, but the general dorsal surface is not sharply separated from the lateral surface; otic notch closed at junction of squamosal and tabular; step anterior to canine as in predaceous Pelycosaurs; quadrate situated below plane of maxillary teeth; maxilla with its large canine crowds out lacrimal to form a junction with the nasal as in the advanced Pelycosaurs; squamosal covers most of posterior face of the quadrate; choanae well forward; expansion of posterior end of prevomer; quadrate ramus of pterygoid reaching quadrate; epipterygoid narrow, but not a typical *columella cranii* and reaches parietal; quadrate in contact with paroccipital; angular notch as in Sphenacodontidae.

The Pristerognathids differ from the Pelycosaurs: the parietal separates the postorbital from the squamosal; there is no basal movable articulation; the palate is not Rhynchocephalian-like; supratemporal absent; dorsal surface not sharply demarcated from lateral surface and sides not steep; premaxilla not extending posteriorly between nasals; parietal short but narrow; upper edge of occiput not moved forward and occiput is thus not slanting and the surface of the interparietal and tabular are not visible in dorsal view; condyle and quadrates not in posterior position; lacrimal always with little anterior extent; the postorbital bar is always slender, never developed as a plate of bone between orbit and temporal fossa; maxilla never meets quadratojugal; jugal though extending far posteriorly never meets the quadratojugal; quadratojugal always very small; septomaxilla with large facial exposure; only the anterior ramus of the pterygoid bearing teeth and no teeth on the lateral pterygoidal flange nor any on the palatine and ectopterygoid; lateral pterygoid flange never meeting the jugal; suborbital vacuity always present and large; epipterygoid somewhat broader and reaching the parietal; angular notch present and dentary always with a strong coronoid process.

It will furthermore be of interest to note in what characters the Pristerognathids agree with the Cynodonts viz. dentary with large coronoid process; sloping mentum; interparietal region narrow and sagittal crest; postorbital does not meet squamosal; preparietal absent; posterior end of prevomer spatulate and underlying palatines and pterygoids; jugal stretching far posteriorly ventral to the anterior ramus of the overlying squamosal; frontal sometimes excluded from orbital border as in Cynodonts.

REFERENCES

Boonstra, L. D. 1934. A Contribution to the Morphology of the Mammal-like Reptiles of the Suborder Therocephalia. Ann. S. Afr. Mus. XXXI, pp. 215-267.

Boonstra, L. D. 1935. On Some South African Reptiles of the Suborder Therocephalia preserved in the American Museum of Natural History. Am. Mus. Nov. 771, pp. 1-12.

Boonstra, L. D. 1953. The Lower Jaw Articulatory Region in some Pristerognathid Therocephalians. Ann. S. Afr. Mus. XLII, 1, pp. 54-63.

Broom, R. 1903. On Some New Primitive Theriodonts in the South African Museum. Ann. S. Afr. Mus. IV, pp. 147-158.

Broom, R. 1904. On Two New Therocephalian Reptiles (*Glanosuchus macrops* and *Pristerognathus baini*). Trans. S. Afr. Phil. Soc. 15, pp. 85-88.

Broom, R. 1915. On Some New Carnivorous Therapsids in the Collection of the British Museum. Proc. Zool. Soc., pp. 163-173.

Broom, R. 1915. Permian, Triassic and Jurassic Reptiles of South Africa. Bull. Am. Mus. Nat. Hist. XXV, II, pp. 105-164.

Broom, R. 1925. On some Carnivorous Therapsida. Rec. Alb. Mus. III, pp. 309-326.

Broom, R. 1931. Notices of some new Genera and Species of Karroo Fossil Reptiles. Rec. Alb. Mus. IV, pp. 161-166.

Haughton, S. H. 1918. Some New Carnivorous Therapsida, with Notes upon the Brain-Case in Certain Species. Ann. S. Afr. Mus. XII, p. 175-216.

Seeley, H. G. 1895. On the Therosuchia. Phil. Trans. Roy. Soc. 185, pp. 987-1018.

8. *The Cranial Structure of the Titanosuchian: Anteosaurus.* By L. D. Boonstra, D.Sc.

(With 22 text-figures.)

Historical

Although the *Anteosaurus* skull was first described by Broom as long ago as 1910, the details of the cranial structure are still very inadequately known.

Watson in 1914 gave some details of the structure of the incomplete skull in the British Museum and in 1921 the same author, giving details of the snout, instituted the name *Anteosaurus* for the specimen hitherto thought to be a *Titanosuchus*.

Broom in 1929 founded an additional species — *A. minor* — on a piece of the skull roof.

Broili and Schröder in 1935 described certain skull fragments under the name *Titanognathus lotzi*.

In 1936 the present author figured and described a distorted skull of *A. minor* that had been sold to the American Museum by Dr. Broom.

In the same year Broom described a good skull and lower jaw under the name *Dinosuchus vorsteri*.

In 1948 the present author published a figure of a skull, which in 1952 was named *A. abeli*, and in 1953 a taxonomic account of the Titanosuchians included a number of photos of *Anteosaurus* skulls in the South African Museum.

Material

The present paper is based mainly on the large number of specimens in the collection of the South African Museum, viz.

S.A.M. 2752. Vivier Siding, Beaufort West. Coll. Haughton & Whaits. Posterior two thirds of the skull without basis cranii.

S.A.M. 4340. Leeurivier, Beaufort West. Coll. Haughton. A good skull, though distorted by a simple shear, with part of the lower jaw.

S.A.M. 5621. Leeurivier, Beaufort West. Coll. Haughton. A snout and part of the skull roof.

S.A.M. 9123. Voëlfontein, Prince Albert. Coll. Boonstra. A weathered skull.

S.A.M. 9139. Voëlfontein, Prince Albert. Coll. Boonstra. A weathered skull fragment.

S.A.M. 9140. Voëlfontein, Prince Albert. Coll. Boonstra. A partial disarticulated skull.

S.A.M. 9329. Kruisvlei, Beaufort West. Coll. Boonstra. A good skull and much of the lower jaw.

S.A.M. 11293. Boesmansrivier, Beaufort West. Coll. Boonstra. A good weathered skull, slightly dorso-ventrally compressed and distorted, with some bones of the occiput disarticulated.

S.A.M. 11296. Kruisrivier, Sutherland. Coll. Boonstra & Laurenson. A very good skull and lower jaw, though somewhat distorted by a simple shear.

S.A.M. 11302. Buffelsvlei, Beaufort West. Coll. Boonstra & Marais. A fair, weathered skull and lower jaw.

S.A.M. 11492. Mynhardtskraal, Beaufort West. Coll. Boonstra. A fairly complete skull without lower jaw.

S.A.M. 11576. Klein-Koedoeskop, Beaufort West. Coll. Boonstra. A snout with fairly well preserved teeth.

S.A.M. 11577. Bulwater, Beaufort West. Coll. Boonstra & Truter. A good practically undistorted three quarters of a well preserved skull.

S.A.M. 11592. Dikbome, Laingsburg. Coll. Boonstra & Du Plessis. A weathered skull, but with a good palatal region.

S.A.M. 11694. Koringplaas, Laingsburg. Coll. Boonstra & Du Plessis. A very good undistorted skull without the lower jaw.

S.A.M. 11929. Kruisvlei, Beaufort West. Coll. Boonstra. The greater part of a skull in intractable matrix.

S.A.M. 11946. Buffelsvlei, Beaufort West. Coll. Boonstra & Marais. A nearly complete, good skull, slightly distorted by a simple shear.

S.A.M. 11949. Nuwefontein, Fraserburg. Coll. Boonstra & Jooste. A partial skull, snout and occiput not in contact.

General Skull Form

There is some difficulty in determining the correct skull form in *Anteosaurus,* due to the post-mortem deformation the available material has usually undergone. In only one skull (S.A.M. 11694) there appears to be little disturbance of the original symmetry. In 8 the deformation is chiefly due to dorso-ventral pressure, but accompanied by some measure of distortion. In 5 specimens the skulls have been subjected to a shearing action — mostly in the form of a simple shear. In these sheared specimens it is of interest to note that they were all lying on their left sides. In only 1 specimen, lying on its right side, the deformation was due almost wholly to compression from side to side.

In the figures the legend indicates where an attempt has been made to correct the effects of the deformation. The resulting correction made from the dorsal and ventral aspect has in some cases not produced the same result and a mean between the two results may indicate the correct condition, but not necessarily so.

The *Anteosaurus* skull is large to very large (480-800 mm. max. length; 222-612 mm. max. width). The snout (with the mandible) is much higher than broad and thus, notwithstanding the width over the temporal region, the skull gives the impression of being high and narrow. This is in sharp contrast to the other Titanosuchians and the Tapinocephalia. In those specimens where the incisors are present the carnivorous nature is strongly evident. The prominent boss-like development of the upper part of the postorbital bar is striking, and in some specimens this rugged appearance is further strengthened by the presence of bosses on the jugal and angular and around the pineal foramen with a lesser or greater amount of swelling of the frons. The great lateral and posterior sweep of the temporal arches is characteristic; the temporal fossa is large and extends far ventrally with a relatively narrow infra-temporal arch. The ventral postero-lateral corner of the skull is not formed by the quadratojugal lying on the surface, but, lying medially, gives an un-Deinocephalian-like appearance to the *Anteosaurus* skull.

The orbits are of medium size and face anterolaterally; the nostrils are non-terminal and lie laterally, whereas in all other Deinocephalians they are directed much dorsally. The intertemporal region is fairly narrow, but without any suggestion of a sagittal crest. The mentum of the lower jaw is high and squarish.

The anterior part of the dentigerous border of the upper jaw sweeps sharply upwards, exposing the long intermeshing incisor teeth.

The lower jaw is hinged fairly far posteriorly.

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a. The Skull in Lateral View (Figs. 1, 6, 8, 11, 17)

In lateral view the skull is roughly pearshaped in outline. The preorbital portion is much longer than the postorbital part. The lateral direction of the nostril, orbit and temporal opening is apparent. The temporal opening extends far ventrally and the infratemporal bar is narrow. The quadrato-jugal is not a bone of the surface but lies medially of the postero-lateral corner of the skull. The side of the snout is fairly vertical.

The Premaxilla (P.M.) forms the anterior $\frac{1}{4}$ of the upper edge of the skull; anteriorly it has a rounded curve to the dentigerous border, which curves

sharply upwards in antero-posterior direction; from the nostril a groove in the surface of the bone runs anteriorly, lying above the curved premaxilla-maxillary suture; on the lower border of the nostril the premaxilla is separated from the septomaxilla by a narrow tongue of the maxilla; the anterior $\frac{1}{2}$ of the internarial bar is formed by a strong girder of the premaxilla, but in the posterior half the nasal helps in forming the internarial bar;

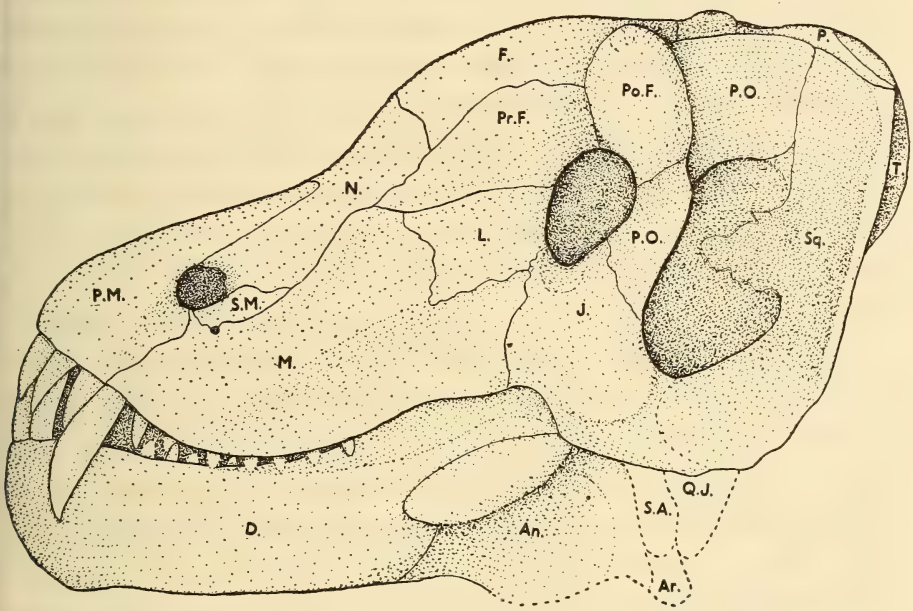


FIG. 1.—*Anteosaurus abeli.* Holotype. S.A.M. 11296. Kruisrivier, Sutherland. Lateral view of the left side of the skull. ($\times \frac{1}{6}$.) The distortion due to a simple shear corrected. In this and all the other figures, orthoprojections, obtained with a pantograph, are given. In the lateral views the projection is on the median plane. In the dorsal and ventral views the projection is on the plane in which the postcanines lie. In the occipital views the projection is at right angles to the plane of the postcanine alveolar border.

An.—angular; Ar.—articular; B.O.—basioccipital; B.S.—basisphenoid (sheathed by parasphenoid); D.—dentary; E.O.—exoccipital; F.—frontal; I.P.—interparietal; J.—jugal; L.—lacrimal; M.—maxilla; N.—nasal; P.—parietal; Pal.—palatine; P.M.—premaxilla; P.O.—postorbital; P.O.c.—paroccipital; P.V.—prevomer; Po.F.—postfrontal; Pr.F.—prefrontal; Pt.—pterygoid; Q.—quadrate; Q.J.—quadratojugal; S.A.—surangular; S.M.—septomaxilla; S.O.—supraoccipital; Sq.—squamosal; St.—stapes; T.—tabular; Tr.—transversum.

posteriorly the premaxilla has a wedge-shaped prolongation into the nasal, extending posteriorly of the nostril roughly for the length of the nostril, or in some cases for double this length. The premaxilla is either edentulous or carries a variable number of incisor teeth (1-5), with the number sometimes varying in the two premaxillaries of the same skull. There is a considerable variation in the length of the dentigerous border of the premaxilla, even within what I consider to be the same species; this variation is concomitant

with both the number and size of the incisor teeth; in *A. abeli,* S.A.M. 4340, the dentigerous edge on the left side with 5 incisors is 160 mm., whereas in S.A.M. 11296 with 3 teeth it is 90 mm., and in the right size with 4 teeth it is 110 mm.

The Septomaxilla (S.M.) has a small facial exposure; dorsally it forms the posterior part of the lower narial border; curving sharply inwards it extends to near the median line to form the floor of the nostril. Anteriorly it does not meet the premaxilla, being separated from this bone by a narrow tongue of the maxilla. Posteriorly it extends as a short wedge in between the nasal and maxilla. There is a small septomaxillary foramen.

The Nasal (N.) is in lateral view seen to be a long narrow bone with a constricted waist. Anteriorly it forms the posterior border of the nostril, with a dorsal prong extending in to the dorsal narial border and a ventral prong extending in to the ventral narial border. Posteriorly it extends to about halfway the swelling of the forehead, where it meets the frontal in a feebly sigmoid suture.

The Maxilla (M.) is a large bone extending far posteriorly, where it overlaps the jugal. In the smaller forms, e.g. *A. cruentus* (S.A.M. 11694), it does not in its ventral part stretch so far posteriorly as in the larger forms, so that in the former the suture with the jugal is oblique, whereas in the latter it is vertical. On the surface of the maxilla there is a strong ridge running obliquely from the orbit in the direction of the canine. In its dorso-posterior part the maxilla has a triangular tongue which separates the jugal from the lacrimal except for a short distance near the orbit. The maxilla carries a variable number of teeth (5-8), often irregularly spaced.

The Frontal (F.) forms in lateral view the middle portion of the dorsal edge of the skull. It forms the major portion of the fore-head swelling, as this is varyingly developed in the different forms. The frontal has a small tonguelike entry into the dorsal orbital border, except in S.A.M. 11296 where the large postfrontal boss overlaps it.

The Prefrontal (Pr.F.) has in lateral view a curved dorsal edge and a fairly straight ventral edge. Anteriorly it stretches as a wedge between the nasal and maxilla, and posteriorly it forms the thickened anterodorsal part of the orbital border. It forms the lateral part of the forehead swelling and, where this is great, it forms an overhanging bulge.

The Lacrimal (L.) varies in size, due to the extent to which the maxilla extends posteriorly. It is a roughly quadrilateral bone with a short suture with the jugal and forming the anterior part of the orbital border. Its suture with the prefrontal lies on a fairly sharp ridge.

The Jugal (J.) is quite a large bone notwithstanding the encroachment of the maxilla anteriorly. It forms the lower orbital border and extends a little on to the anterior as well as the posterior orbital border. It has only a small

contact with the lacrimal. Entering the postorbital bar it is greatly overlapped by the postorbital. It has a long and strong posterior process which, in the form of a sheet of bone, forms the inner surface of the zygomatic arch and extends posteriorly to past the quadratojugal. The outer surface of the process is overlapped by the zygomatic process of the squamosal. The amount of this overlap varies in the different forms. In *A. cruentus* (S.A.M. 11694) the outer surface of the jugal, below the orbit, is fairly smooth, except for a hollow which is present in all forms immediately below the orbital border, but in the larger forms there is a swelling, feeble in *A. abeli* (S.A.M. 4340), low in *A. abeli* (S.A.M. 11296) and *A. vorsteri* (S.A.M. 11577) and strong and prominent in *A. crassifrons* (S.A.M. 11946 and S.A.M. 11302) and *A. acutirostris* (S.A.M. 9329) where it forms a prominent overhanging outgrowth.

The Postfrontal (Po.F.) forms the large and prominent boss-like growth overhanging the postero-dorsal orbital border. The size of this boss determines the amount of its overgrowth over the surface of the frontal and the size of the entry of the frontal tongue into the dorsal orbital border. Ventrally the extent of the pachyostosis in the postfrontal determines the degree to which it overlaps the postorbital on the postorbital bar so that the position of the postfrontal-postorbital suture shows a considerable variation. In the forms where the thickening of the frontal is not very great the postfrontal forms part of the dorsal outline of the skull when observed in lateral view; in the other forms it nearly reaches the dorsal edge or lies well below it.

The Postorbital (P.O.) presents, in lateral view, two distinct surfaces. The more lateral surface is exposed where the bone forms the fairly weak and narrow curved part of the postorbital bar overhung to a greater or lesser extent by the bosslike postfrontal. In a more medial plane the postorbital provides the sheet of bone which forms the lateral face of the intertemporal region and forms the dorsal edge of the temporal fossa. There is a considerable variation in the size and shape of this plate of bone. Posteriorly it meets the upsweeping arm of the squamosal in a long suture. Ventrally its edge overhangs the squamosal where this bone forms the inner face of the temporal fossa.

The Parietal (P.) is in lateral view seen only where it presents the lateral surface of the pineal boss and its long postero-lateral tongue intercalated between the squamosal and tabular. It does not form the upper inner face of the temporal fossa as it is here covered by the postorbital which forms the inner face of the fossa.

The Tabular (T.) in lateral view is seen to form the postero-dorsal border of the posttemporal arch and in some forms the tabular is also seen as it

descends on the posterior surface forming the prominent ridge limiting the occiput proper.

The Squamosal (Sq.) is a large bone of intricate shape. In lateral view it is seen to form the lateral part of the posttemporal arch and the greater part of the inner surface of the temporal fossa, except for that part formed by the postorbital, and the outer surface of most of the zygomatic arch. Anteriorly it meets, within the temporal fossa, the postorbital, and lower down the supraoccipital and paroccipital. In the angle between the zygomatic process and the inner facing of the temporal fossa the squamosal also forms the niche in which the upper and hinder faces of the quadrate are housed.

The Quadratojugal (Q.J.) is not preserved in most of the specimens, but in the four skulls in which it is preserved, its lateral surface appears to be triangular in outline and this does not lie on the surface of the postero-ventral outer corner of the skull as it does in all other known Deinocephalia, but lies in a plane medial to the subtemporal arch as in Therocephalians, Gorgonopsians, and the higher Therapsids. The quadratojugal rests on a ledge of the quadrate above the outer quadratic condyle. In these relations it approaches very closely to the condition recently described by me in the contemporary Pristerognathid Therocephalians. In one skull of *A. cruentus* (S.A.M. 11694) there is a small notch in the squamosal lying lateral to the quadratojugal.

Palatal bones. When the lower jaw is disarticulated the lateral surfaces of some of the palatal bones are seen. The lateral surface of the lateral flange of the pterygoid (Pt.), the quadrate ramus of the pterygoid and of the anterior pterygoid process, the transversum and palatine are all visible. In *A. cruentus* (S.A.M. 11694) the basisphenoid is also partly seen.

Noteworthy are the strong and deep pterygoidal flange and the prominent dentigerous boss on the palatine.

b. The Skull in Dorsal View (Figs. 2, 7, 9, 10, 14, 18, 21, 22)

In dorsal view the *Anteosaurus skull* presents in outline a pear-shaped form, with the jugal bosses in some forms appearing as lateral protuberances, in some cases low and in others prominent. In *A. crassifrons* the skull is short and squat with a relatively broad snout. In the others the snout is either narrow, fairly narrow or moderately wide. The forehead swelling is low, moderate to very massive. In all the postfrontal boss on the dorsal part of the postorbital bar is prominent. In *A. acutirostris* (S.A.M. 9329) and *A. crassifrons* (S.A.M. 11946) the jugal boss protrudes strongly beyond the general skull-outline; in *A. abeli* (S.A.M. 11296) and *A. vorsteri* (S.A.M. 11577) moderately, and in the others not at all.

The orbits are in all cases only partly visible, being overhung by the fore-head swelling; in *A. cruentus, A. abeli* and *A. vorsteri* this overhang

is least, in *A. levops* and *A. acutirostris* fairly great and in *A. crassifrons* very great.

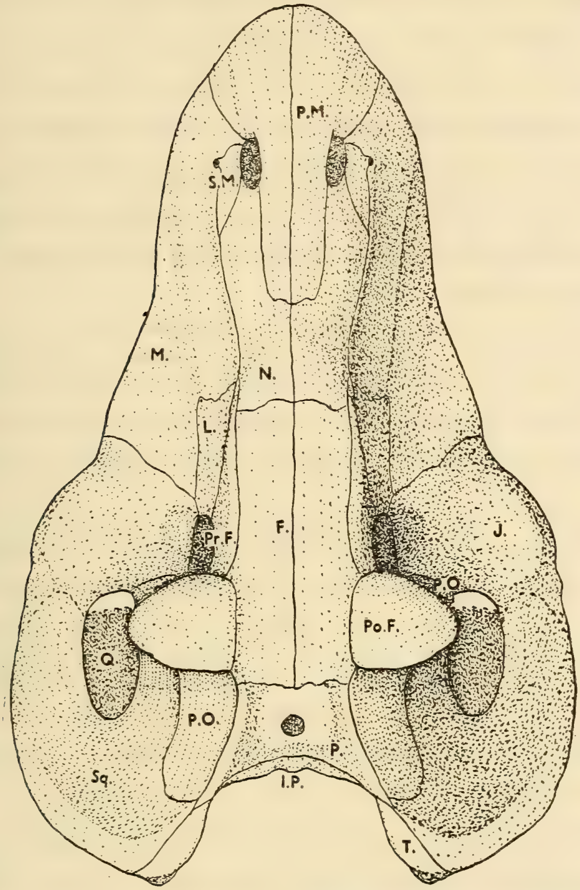


FIG. 2.—*Anteosaurus abeli*. Holotype. S.A.M. 11296, Kruisrivier, Sutherland. Dorsal View with distortion due to a simple shear corrected. ($\times \frac{1}{6}$.)

The temporal fossa is broad and long with the temporal arches flaring greatly laterally and posteriorly. The occipital edge is deeply concave from side to side. The intertemporal region is generally flat, but with a pineal boss varying from low to prominent and massive. The intertemporal width is small, medium to fairly broad with no suggestion of the development of a sagittal crest. The pineal foramen is fairly small and situated near, to very near, the occipital edge. The internarial bar is strong and massive.

The Premaxilla (P.M.). The two premaxillaries together form the rounded anterior margin of the skull. Laterally they meet the maxilla in a curved

suture lying lateral to a groove in the premaxillary surface. The premaxilla forms the anterior and most of the dorsal narial border. Together they form a stout internarial bar, which, extending backwards for only a short distance, is posteriorly abruptly truncated. This truncation is rather surprising since the premaxilla-nasal suture lies in a groove which is continued to near the fronto-nasal suture. This accounts for the error of observation on my part as depicted in the figure of the specimen in the American Museum, which later in this paper is made the type of a new species, *A. minusculus*.

The Septomaxilla (S.M.) is as already described in lateral view.

The Maxilla (M.), in addition to the features described when seen in lateral view, shows clearly that the suture between it and the septomaxilla and nasal lies along a curved ridge.

The Nasal (N.). The paired nasals are hourglass-shaped in outline, with the truncated posterior end of the premaxillaries separating them in their anterior half to a third. The posterior part of the nasals enters the fore-head swelling to a greater or lesser extent depending on the development of this thickening. Where the frontal swelling is least, the nasal extends furthest posteriorly.

The Frontal (F.). The paired frontals form a more or less pronounced cruciform figure with the narrow tongues entering the orbital borders forming the cross member. In two cases this cross member is truncated and on the surface does not enter the orbital border. The postfrontal boss overflows on to the frontal surface to a varying extent. Posteriorly the frontals meet the parietals in a suture running across the skull just anterior to the pineal boss, but in *A. crassifrons* the pineal boss extends anteriorly as a strong swelling on to the posterior part of the frontals. The frontals meet the edge of the postorbitals posterior to the limits of the postfrontals.

The Prefrontal (Pr.F.). In dorsal view the extent to which the prefrontal enters the fore-head swelling is indicated in the figures. Where this swelling is least developed the overhang of the prefrontal over the orbit and the lateral skull face immediately anterior to the orbit is least and the transition from the dorsal to the lateral surface not very abrupt. Whereas in *A. crassifrons* the swollen prefrontal all but obscures the lacrimal from dorsal view.

The Lacrimal (L.) is as described in lateral view, except that in dorsal view it is overhung by the prefrontal swelling to a greater or lessor extent depending on the amount of the pachyostosis of the prefrontal.

The Postfrontal (Po.F.). In dorsal view the knob-like bosses formed by the greatly thickened postfrontals are a very prominent feature. In most skulls this boss completely overhangs the part of the postorbital entering the postorbital bar; in others the lower part of the postorbital above the suture with the jugal is visible, and in three cases the boss leaves exposed, behind

its posterior edge, the postorbital as it sweeps from the upper temporal face down to the lower part of the postorbital bar.

The Parietal (P.) has a relatively small dorsal surface. The two bones are fused except where they are pierced by the fairly small pineal foramen. Round the pineal foramen the parietals are thickened to form a boss variable in size and shape. In some skulls a distinct ring wall with sharp edges surrounds the foramen, in others only a low mound is formed, whereas in *A. crassifrons* a massive thickening extends into the frontals and in *A. vorsteri* (S.A.M. 11577) the frontal surface, anterior to the low boss, is slightly hollowed out in the form of a V shaped depression bounded by a low ridge. In one specimen (S.A.M. 2752) the pineal boss overhangs the occiput. The pineal foramen is near or very near the posterior edge of the parietals.

Posteriorly each parietal sends out a long horn with its end wedged in between the dorsal end of the tabular and the upper part of the squamosal. The outer edge of the parietal horn forms a sharp ridge lying lateral to a groove and thus sharply demarcating the intertemporal surface.

The Postorbital (P.O.). The posterior flange of the postorbital is a large sheet of bone applied to the outer surface of the parietal and, extending far back, it is met by the upsweeping squamosal. The ventral edge of the postorbital flange overlaps and overhangs the antero-medially directed sheet of the squamosal.

Little of that part of the postorbital which helps to make up the postorbital bar is usually seen in dorsal view, being overhung by the greatly swollen postfrontal.

The Jugal (J.). In dorsal view the boss of the jugal, in those forms where it is developed, is shown very clearly as it determines the outline of the skull in this region.

The Squamosal (Sq.) in dorsal view presents a zygomatic process covering the latero-dorsal surface of the long zygomatic process of the jugal. From this level the squamosal sweeps upwards to form the postero-lateral part of the posttemporal arch, where it meets the postero-laterally sweeping horn of the parietal and posteriorly abuts against the tabular. Within the temporal fossa the squamosal forms its large internal surface; dorsally meeting the postorbital and, at a lower level, sweeps antero-medially to meet the supraoccipital and paroccipital. Between the zygomatic process and the antero-medial process a niche in the anterior squamosal surface houses the quadrate.

The Interparietal (I.P.), and *Supraoccipital* (S.O.). In dorsal view little of the occiput is seen as this is vertical. The dorsal edge of the interparietal and in some cases a bit of the surface of the supraoccipital can be seen, and in *A. acutirostris* the occipital condyle.

c. The Skull in Ventral View (Figs. 3, 13, 15, 16, 19)

In general terms it may be said that in the ventral aspect of the skull two surfaces are shown meeting in an obtuse angle at the plane of the transverse pterygoid flanges. Posterior to the very prominent transverse pterygoid flanges the *basis cranii* lies in a more or less horizontal plane, whereas anteriorly the palate is in anterior direction directed upwards. This is accentuated by the upward retreat of the alveolar border of the premaxillaries. The most prominent features in the ventral aspect of the skull are: the strong and deep lateral flanges of the pterygoid, the strong reniform dentigerous bosses of the palatines, the retreat of the alveolar border

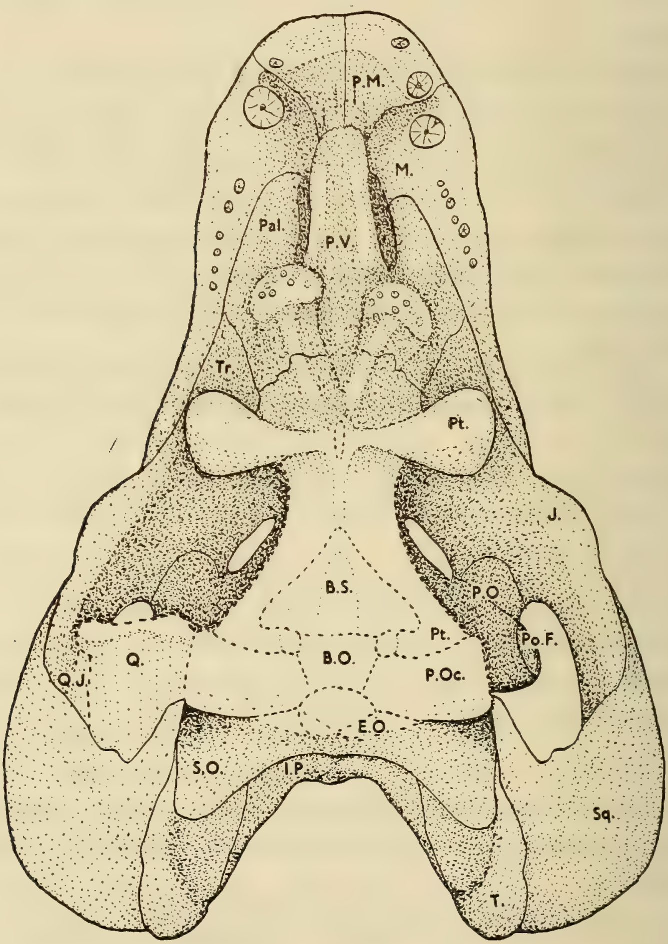


FIG. 3.—*Anteosaurus vorsteri*. Referred specimen. S.A.M. 11577, Bulwater, Beaufort West. Ventral View. (× $\frac{1}{6}$.)

of the premaxillaries, the medial shift of the quadratojugal away from the lateral surface of the skull and the deeply concave occiput.

The Premaxilla (P.M.) has an alveolar border and a palatal process. The alveolar border has retreated upwards. It carries a variable number of teeth — 5, 4, 3. The number of incisors in the two premaxillaries of the same skull is, in some cases, unequal. Where no teeth roots are preserved there is a groove in the alveolar surface which is either clearly separated into separate alveoli, or not. The palatal process meets the prevomers which underly it, and laterally meet the maxilla along a curved suture.

The Maxilla (M.). Ventrally the maxilla has, in addition to its alveolar edge, a medially directed tongue which separates the premaxilla from the palatine and except in *A. crassifrons* makes contact with the prevomer. Antero-medially of the upper canine the maxilla is deeply excavated to receive the fang of the lower canine. The maxilla carries a large canine and a variable number of postcanines. The latter are irregularly spaced and vary in size and in number (5-8). The root cross-sections show the postcanines to be rather feeble teeth of no great functional importance.

The Prevomer (P.V.). The pair of prevomers form a strong interchoanal bar, anteriorly underlying the palatal process of the premaxillaries and posteriorly tapering in between the palatines to make a small contact with the pterygoids. The interchoanal bar is, except anteriorly, deeply excavated longitudinally and each prevomer has a well defined ridge on its lateral edge, which forms the medial border of the slitlike choanae.

The Palatine (Pal.) meets the maxilla in a long suture lingually of the alveolar border and curving upwards forms most of the lateral and posterior border of the choana. Further back it carries a strong and prominent reniform dentigerous boss. In most cases the fair-sized recurved teeth are implanted in a single curve but in *A. vorsteri* (S.A.M. 11577) there appears to be a double row. Posterior to the boss there is a ridge continued on the pterygoid towards the interpterygoidal slit.

The Transversum (Tr.), composed of a sheet of bone lying antero-laterally of the pterygoid flange, meets the palatine, maxilla and jugal and descending along the front and side of the pterygoid flange forms the upper part of the lateral and part of the anterior face of the strong lateral pterygoid flange. There is no fenestra between the transversum and palatine.

The Pterygoid (Pt.) has the usual complex form of the Therapsids. The anterior process is short, the lateral flange deep and strong, the quadrate process sweeps backwards with a straight outer edge and in the middle line the pterygoids together form a fairly deep keel posterior to the interpterygoidal slit. In the fork between the two quadrate rami the pterygoids meet the basisphenoid (basi-parasphenoid) in a U-shaped suture with no development of basipterygoid processes.

In most skulls the posterior extremity of the quadrate ramus is not adequately preserved and its relations with the quadrate uncertain. But in a specimen which I believe to be an *A. crassifrons* (S.A.M. 11929) it would appear that the quadrate ramus of the pterygoid is applied to the inner face of the quadrate a little below the distal end of the stapes. If this observation is correct then the condition is very similar to that in *Jonkeria* and in the Tapinocephalids generally.

The Basisphenoid (B.S.) is apparently sheathed along its under surface by the parasphenoid and presents a ventral surface cup-shaped in outline. Just behind the median pterygoidal keel the median basisphenoidal surface is excavated to form a broad groove, which is continued in the basioccipital right up to the condyle. Lateral to the median groove the basisphenoid develops a rounded ridge which broadens posteriorly until it is posteriorly notched and develops a latero-posteriorly directed tongue, which forms the antero-ventral border of the *fenestra ovalis*. The basioccipital-basisphenoidal suture runs across the median groove from notch to notch. The basisphenoidal-pterygoid suture runs along the lateral border of the rounded basisphenoidal ridge.

The basisphenoid is a short bone, but in *A. major* (S.A.M. 11293) it is nearly twice as long as in all the other skulls.

The Basioccipital (B.O.) forms the greater part of the rounded condyle with the exoccipitals forming the postero-lateral corners. In *A. crassifrons* and *A. acutirostris* the exoccipitals are intimately fused to the basioccipital to form a rounded condyle. Anterior to the condyle the under surface of the basioccipital is in its median part hollowed out to form a wide groove which is continued on to the basisphenoid. The vertical plate of the basioccipital anterior to the condyle reported by Broom in *A. vorsteri* is not shown in any of the skulls I have examined and this incorrect statement can thus only be due to an error in observation. Antero-laterally the corner of the basioccipital is bent sharply downwards to form the strong medial border of the *fenestra ovalis*. Postero-laterally the continuation of this prominent ridge round the *fenestra ovalis* is formed by the antero-medial corner of the paroccipital, which has a similarly bent down process. The basioccipital abuts against the paroccipital in a diagonal line of contact.

The Exoccipital (E.O.), besides forming the postero-lateral corner of the condyle, has a lateral process which overlaps the paroccipital and supraoccipital, but is not very clearly shown in any of the skulls examined.

The Paroccipital (P.O.) forms a stout girderlike bone medially butting against the basioccipital and distally applied to the inner face of the quadrate and making contact with the descending sheet of the squamosal. The dorso-lateral corner of the paroccipital bounds the post-temporal fossa, which is anteriorly closed by the sheet of the squamosal forming the inner lining

of the temporal fossa. Dorsally the paroccipital lies against the lower edge of the supraoccipital.

The Jugal (J.) in ventral view shows its inner surface. Its zygomatic process is here clearly seen to extend far backwards and to form the inner part of the arch, whose outer half is formed by the overlapping zygomatic process of the squamosal.

The Squamosal (Sq.) shows its posterior surface as it sweeps downwards to overlap the posterior face of the quadrate and quadratojugal.

The Quadrate (Q.) and *Quadratojugal* (Q.J.). In most of the skulls studied the quadrate complex is missing. It would appear that it fits rather loosely in the notch of the squamosal in which its upper end is housed. There was apparently also little ankylosis in the joint between the paroccipital and the quadrate. The quadrate and quadratojugal form an antero-posteriorly flattened mass of bone carrying two moderate condyli on its lower edge, which lies somewhat diagonally in the skull, with the outer condyle furthest posteriorly. The quadratojugal is small and resting on a ledge above the outer quadrate condyle is applied to the outer edge of the quadrate. It lies well medial of the lateral edge of the skull and is not a bone of the lateral surface as it is in all other known Deinocephalia.

d. The Skull in Occipital View (Figs. 4, 20)

The occiput is vertical, but deeply concave from side to side. The strong tabular ridges bound the occiput proper laterally. Lateral to this ridge lies the posterior surface of the posttemporal arch, and the groove which in higher Therapsids functions as an auditory groove.

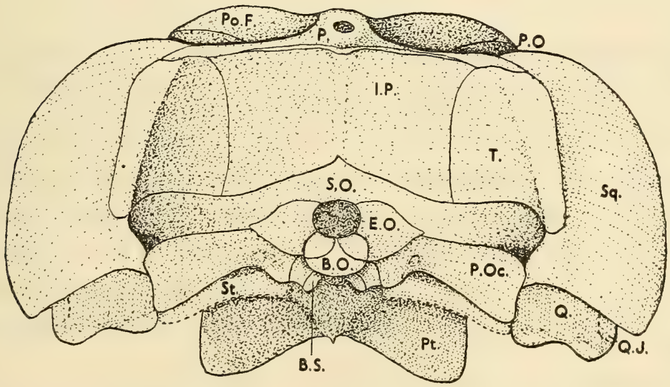


FIG. 4.—*Anteosaurus laticeps.* Sp. Nov. Holotype. S.A.M. 11592, Dikbome, Laingsburg. Occipital View. The possible dorso-ventral compression not corrected. The dorsal part and the quadrate-complex restored from all the other material. ($\times \frac{1}{6}$.)

The Squamosal (Sq.) is seen to form the lateral margin of the skull. Dorsally the squamosal and tabular clasp the extremity of the parietal horn. Ventrally the squamosal overlaps the quadrate and quadratojugal. Medially it makes contact with the tabular in the "auditory groove", which lies lateral to the strong tabular ridge. This ridge is ventrally continued on the squamosal as it fades out. This ridge thus differs materially from the ridge in *Jonkeria*, where the tabular, squamosal and paroccipital contribute to its formation.

The Tabular (T.) carries the strong ridge which forms the inner border of the "auditory groove" and laterally limits the occiput proper. Externally the tabular ridge appears to be sheathed by a thin bone, which I thought may represent the supratemporal, but a number of cross sections in one skull have yielded no evidence to substantiate this. From the ridge the tabular extends medially as a sheet of bone to meet the interparietal. In its dorsal part the occiput consists of 3 layers of bone viz. anteriorly there is a sheet of the squamosal applied to a sheet of the parietal and this is posteriorly covered by the tabular laterally and the interparietal medially.

The Interparietal (I.P.), as a large thin sheet of bone with a ridge in the median line, forms the upper and middle part of the occipital surface.

The Supraoccipital (S.O.) lies below the interparietal and tabular and forms the upper border of the foramen magnum and, laterally, the upper border of the depression which represents the post-temporal fenestra now anteriorly closed by the overgrowing sheet of the squamosal within the temporal fossa. Lateral to the foramen magnum the supraoccipital is overlapped by the exoccipital.

The Exoccipital (E.O.) is seen to form the dorso-lateral segment of the condyle and its lateral flange overlaps the supraoccipital and paroccipital for a short distance.

The Paroccipital (P.O.) is a stout bar between the quadrate and the basioccipital. In posterior view it is clearly shown how its proximo-ventral corner is bent sharply downwards to form the posterior part of the prominent rim of the *fenestra ovalis*. Similarly the downwardly directed processes of the basioccipital and basisphenoid forming the median part of the rim of the *fenestra ovalis* are clearly seen in occipital view. The median groove in the ventral surface of the basioccipital and basisphenoid is also evident.

Stapes (St.) is only partly preserved in one of the skulls studied. It appears to be a stout rod-like bone similar to that of other Deinocephalians but longer.

The Quadrate (Q.) and *Quadratojugal* (Q.J.). In posterior view it is very clear that the quadratojugal has shifted in medial direction as in the higher Therapsids and is no longer a bone of the outer lateral surface of the skull as it is in all other known Deinocephalia.

The Pterygoid (Pt.). In occipital view the deep lateral flanges of the pterygoids are well shown.

The Post-temporal Fenestra does not penetrate the occipital plate as it is anteriorly closed by a sheet of the squamosal. In occipital view it is thus only evident as a depression lying in the corner between the supraoccipital, paroccipital and squamosal.

e. The Lower Jaw (Figs. 1, 5, 6)

Since the quadrate has not shifted much in anterior direction the lower jaw is long. The mandibular ramus is strong and heavy, particularly in its anterior part. In all the larger forms there is a strong and prominent boss on the anterior part of the angular. Unfortunately no lower jaw is preserved in those forms without a jugal boss, but I think it likely that in these cases no angular boss will be developed. In contradistinction to the condition in other Deinocephalia there is in *Anteosaurus* some indication of the development of a low coronoid process to the dentary.

In my material only the outer surface of the mandible is shown exposing the dentary, angular, surangular and articular.

The Dentary (D.) is a massive bone. The mentum is high and fairly upright and the symphysis strongly ankylosed. Posteriorly the dentary curves upwards to form a low incipient coronoid process. The dentary carries a strong canine and a variable number of incisors and postcanines. The number of incisors varies from 2 to 4. The number of postcanines is difficult to determine but seems to vary from 4 to 7.

The Angular (An.) is remarkable for the development on the outer surface of a large egg-shaped swelling in its anterior part. Posterior to the boss the angular has the typical Therapsid structure.

The Surangular (S.A.) is in outer view the typical curved girder-like bone it is in Therapsids generally, but anteriorly it rises and meets the dentary in the low coronoid process.

The Articular (Ar.) has only a small external face forming the extreme postero-ventral corner of the lower jaw.

f. The Dentition (Figs. 1, 5, 6)

The dentition of *Anteosaurus* is clearly that of a specialised type of carnivore. With the large canines, long intermeshing incisors, and feeble postcanines it obviously did no chewing and very little shearing, but was rather well adapted for grabbing and then tearing flesh from its victim, and just before deglutition the lump of flesh was held by the recurved teeth situated on the palatine bosses.

The Anteosaurus-incisors are quite distinct from those in the other carnivorous Therapsids, as for example those usually present in the Therocephalians Gorgonopsians and Cynodonts. In the latter the upper incisors in occlusion lie labially of the lower incisors, whereas in *Anteosaurus* the two sets intermesh as do the herbivorous teeth of the Tapinocephalia. To give the long incisors functioning space the alveolar border of the premaxilla retreats and the upper incisors are directed much anteriorly. The first incisor is smaller than the second and with its fellow forms a distinct pair, as is also the case in the Pristerognathid Therocephalians. This pair passes in between the number one pair of incisors of the dentary. When fully developed there are five upper and four lower incisors, but even in the same skull the number in the two halves is mostly different. So we have, in S.A.M. 11576, 5 left upper, 4 right upper and in both sides 3 lower; in S.A.M. 11296, 3 left upper, 4 right upper and 2 lower on both sides; in S.A.M. 4340, 5 left upper, 4 right upper and 4 left lower; in S.A.M. 11694 no uppers; in *crassifrons* no uppers; in S.A.M. 11577, 2 left and 1 right upper; in S.A.M. 11492, 3 left and no right uppers. In those cases where no incisors or incisor roots are preserved there is in the alveolar border a more or less

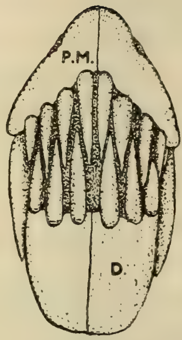


FIG. 5.—*Anteosaurus abeli.* Referred specimen. S.A.M. 11576, Klein-Koedoeskop, Beaufort West. Orthoprojection of the snout on to the plane of the occiput. (× 1/6.)

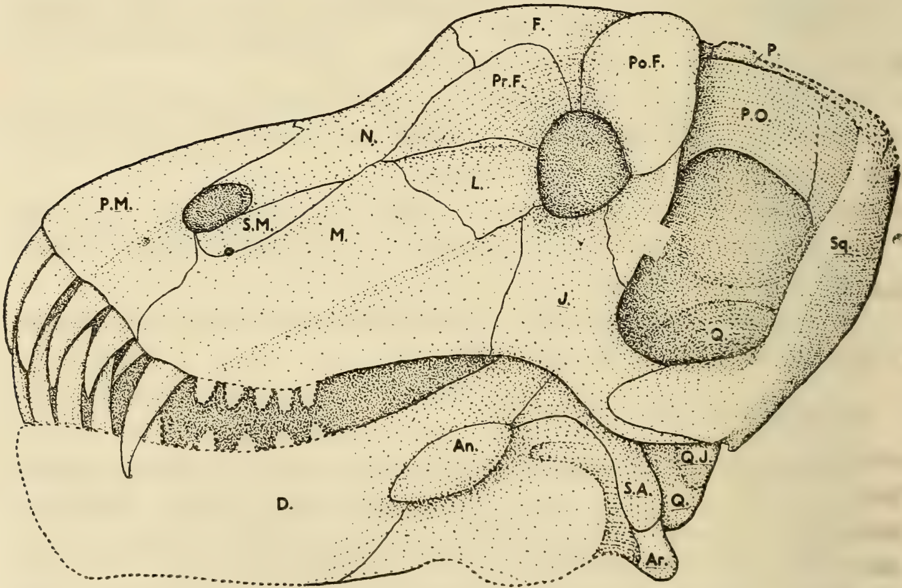


FIG. 6.—*Anteosaurus abeli.* Paratype. S.A.M. 4340, Leeurivier, Beaufort West. Lateral View. (× 1/6.)

distinct groove which in some shows more or less indefinite subdivision into separate alveoli. Without sectioning it is difficult to determine whether some forms were permanently edentulous (rather improbable) or whether the first set has not yet erupted or whether the last set has been shed or whether an antecedent set has been shed and a succeeding set not yet erupted.

In S.A.M. 11296 the left canine is on the point of being shed and the cusp lying posterior to it may be the replacing canine as it does not have the appearance of a postcanine.

The postcanines are not well shown and we usually only have the section of the roots on which to base a count. In S.A.M. 11529 some crowns are well preserved and here the last tooth is a fairly small tooth, 16 mm. long, linguo-labially compressed with diameters 11 and 7 mm. In outline the postcanine is fairly bluntly conical. The postcanines are usually irregularly spaced. Their number sometimes varies in the two maxillaries of the same skull. In the genus the postcanines vary in number from 4 to 8 in the upper jaw.

Taxonomic

In 1921 Watson established the genus *Anteosaurus* on the grounds that a skull in the British Museum (R. 3595) from Tamboerfontein differed from all hitherto known Deinocephalians in the possession of only three incisor teeth and in being the first known Deinocephalian skull in which the upper part of the postorbital bar was strongly swollen to form a very prominent boss.

Subsequent finds have shown that in a series of skulls with the typical boss the number of incisors varies and I propose that as diagnostic character for the genus *Anteosaurus* we should consider only the presence of the typical boss formed by the prefrontal bone.

Accepting this character as diagnostic we have to exclude from the genus *Anteosaurus* the form named *A. minor* by Broom who says of it, "but differs in having only a small thickening instead of a huge boss in the postfrontal region". For this unsatisfactory type, consisting of only the interorbital and intertemporal regions, nomenclatural procedure thus compels one to propose a new generic name. I therefore propose that the skull fragment from Merweville, British Museum (Natural History) R.5742, be known under the generic name *Pseudanteosaurus* gen. nov., genotype *Pseudanteosaurus minor* (Broom).

The specimen in the American Museum of Natural History stated by Broom to be the topotype of the above has, however, well developed bulbous swellings in the upper part of the postorbital bar and must be retained in the genus *Anteosaurus* of which it then constitutes a new species to be named and described later in this paper.

Broili and Schröder's genus *Titanognathus* was based on the following diagnostic characters: "Schädel mit schmaler und steil vom prämaxillaren Kieferrand aufsteigender Schnauze, sehr gross. Praemaxillarer Kieferrand gegenüber dem maxillaren stark in die Höhe gezogen, Symphysenregion des Unterkiefers entsprechend erhöht gegenüber dem rückwärtigen abschnitt des Dentale. Zahnformel: $i.\frac{5}{4(?)}$, $c.\frac{1}{1}$, $p.c.\frac{6}{3+?}$." Restudy of the genotype together with the additional material now known has established that the retreat of the premaxillary edge occurs in *Anteosaurus* and the above dental formula is also within the limits of the genus. The generic name *Titanognathus* thus becomes a synonym of *Anteosaurus* but we may continue to regard this specimen as specifically distinct from the genotype *A. magnificus* under the name *A. lotzi* (Broili and Schröder).

Broom's genus *Dinosuchus* was established on the following diagnostic characters: presence of a dentigerous palatine boss, low position of temporal arch, great width of occiput, large size, dental formula i.4, c.1, p.c.5, huge angular boss. In the large number of skulls now known to fall within the limits set for the genus these above characters are present and any difference in degree cannot be more than of specific value. *Dinosuchus* thus becomes a synonym of *Anteosaurus* and the points in which Broom's specimen differs from the genotype warrant the retention of Broom's specific name, *vorsteri*.

Specific descriptions of the known and new species can now be given:

Anteosaurus magnificus Watson.

Broom, R. 1910. *Titanosuchus ferrox* Owen (in errore).
Watson, D. M. S. 1914. *Titanosuchus ferox* Owen (in errore).
Watson, D. M. S. 1921. *Anteosaurus magnificus* Watson.

Genotype. Incomplete skull. British Museum (Natural History) R. 3595. Tamboerfontein, Beaufort West. Coll. Seeley.

In the type skull the snout was not in contact with the rest of the skull and in his restoration Watson failed to realise that the premaxillary edge curved upwards. This feature of the Anteosaurus skull was first reported by Broili and Schröder and confirmed in all subsequent specimens. Due to the incompleteness of the type skull only an incomplete description can be given for the species viz.:

Skull large; maximum length about 660 mm. Snout long, fairly high and wide. Intersquamosal width not great (360? mm.). Postfrontal boss huge and prominent. Jugal and angular bosses unknown. Fronto-naso-prefrontal swelling fairly weak. Pineal boss prominent with sharp circular border, situated very near occipital edge. Degree of upward inclination of premaxillary edge uncertain. The occiput is fairly high, fairly wide, deeply

concave with a great posterior sweep of the temporal arches and the upper part of the temporal fossa roomy antero-posteriorly; the temporal arch rises well above the plane of the intertemporal surface. Palate probably long.

Basis cranii unknown. Condyle unknown. Watson gives the upper teeth as i.3, c.1, p.c. 8 on both sides, but Broom states that there may be 5 incisors.

Anteosaurus lotzi (Broili and Schröder).

Broili, F. and Schröder, J. 1935. *Titanognathus lotzi* Broili and Schröder.

Boonstra, L. D. 1953. *Anteosaurus lotzi* (Broili and Schröder).

Holotype. Skull fragments and some postcranial bones. Alte Akademie, München. No. ?. Brakwater, Beaufort West. Coll. Schröder.

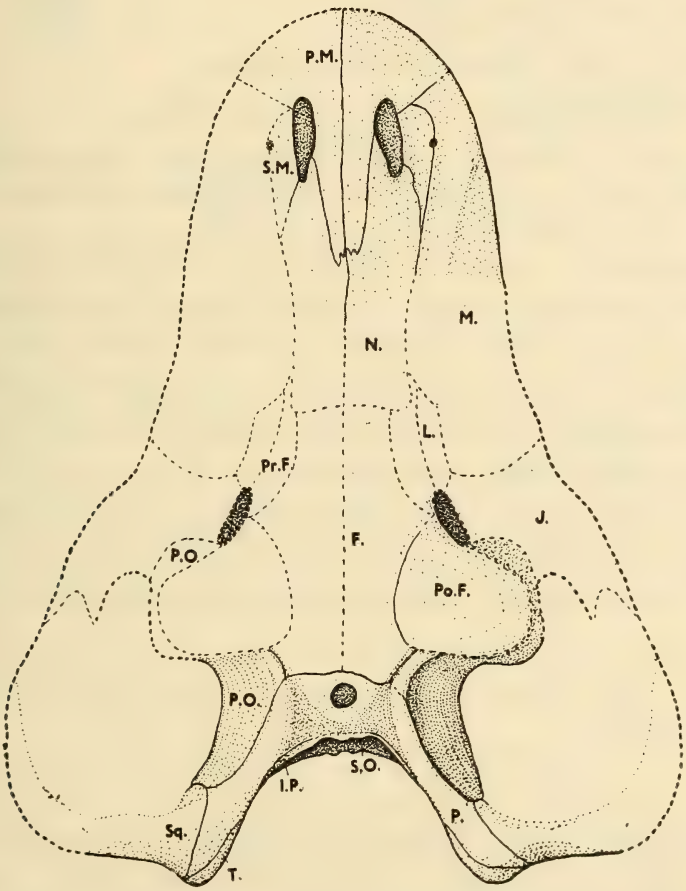


FIG. 7.—*Anteosaurus abeli*. Referred specimen. S.A.M. 11949, Nuwefontein (Roxana), Fraserburg. Dorsal view. This was the first skull in which the truncated posterior limit of the premaxillaries was determined. (× $\frac{1}{6}$.)

As the type is rather unsatisfactory, consisting of only a fragmentary snout, mandibular fragments, incomplete ilium, pubis and femur, only a very incomplete diagnosis can be given viz.:

Skull size unknown, probably large. Snout length unknown, fairly high and narrow. Intersquamosal width unknown. Postfrontal boss unknown. Jugal boss unknown, angular boss strong. Fronto-naso-prefrontal swelling unknown. Pineal boss unknown. Sharp upward inclination of premaxillary edge, and Broili and Schröder record an accompanying step-up of the precanine border of the dentary. The occiput is unknown. Palate unknown. *Basis cranii* unknown. Condyle unknown. Broili and Schröder give the dental formula i.$\frac{5}{4?}$, c.$\frac{1}{1}$ p.c.$\frac{6}{3+?}$.

Anteosaurus vorsteri (Broom).

Broom, R. 1936. *Dinosuchus vorsteri* Broom.

Boonstra, L. D. 1953. *Anteosaurus vorsteri* (Broom).

Holotype. A good skull and part of the lower jaw. Transvaal Museum. 265. Stinkfontein, Prince Albert. Coll. Vorster, Botes and Broom.

Skull very large; maximum length 740 mm. Snout fairly long, high and wide. Intersquamosal width very great (600 mm.). Size of postfrontal boss unknown, probably fairly strong. Jugal boss unknown, angular boss very strong. Fronto-naso-prefrontal swelling unknown, probably fairly weak. Pineal boss unknown, near? occipital edge. Sharp upward inclination of premaxillary edge. The occiput is high, wide, moderately deeply concave, with a fairly great posterior sweep of the temporal arches and the upper part of the temporal fossa roomy antero-posteriorly; the temporal arch not rising above the plane of the intertemporal surface. Palate fairly long, with deep lateral pterygoidal flanges not massive with sharp ventral edge. *Basis cranii* short, with short basisphenoid. Exoccipitals fused with basioccipital to form a rounded condyle. Broom gives the upper teeth as i.4, c.1, p.c.5.

Referred Specimen. (Figs. 3, 8, 9.) A good skull, but lacking the *basis cranii*. S.A.M. 11577. Bulwater, Beaufort West. Coll. Boonstra and Truter.

Those areas of the outer skull surface lost by weathering in the type specimen are here perfectly preserved and the description of this species can thus be augmented as follows: postfrontal boss fairly strong, but not obscuring the lower part of the postorbital in dorsal view; jugal boss low and small: fronto-naso-prefrontal swelling weak, running evenly on to the anterior nasal surface and with little overhanging of the sides of the skull; pineal boss low, with rounded edges not near occipital edge, with hollow on frontal anterior

to the boss; palatine bosses reniform, not circular as described by Broom; in the left premaxilla stumps of two incisors are preserved and on the right one; for the rest the alveolar border presents a matrix filled groove with little indication of separate alveoli; on the left there appears to be room for 5 and on the right for a total of 4 incisors; on the left alveolar border of the maxilla

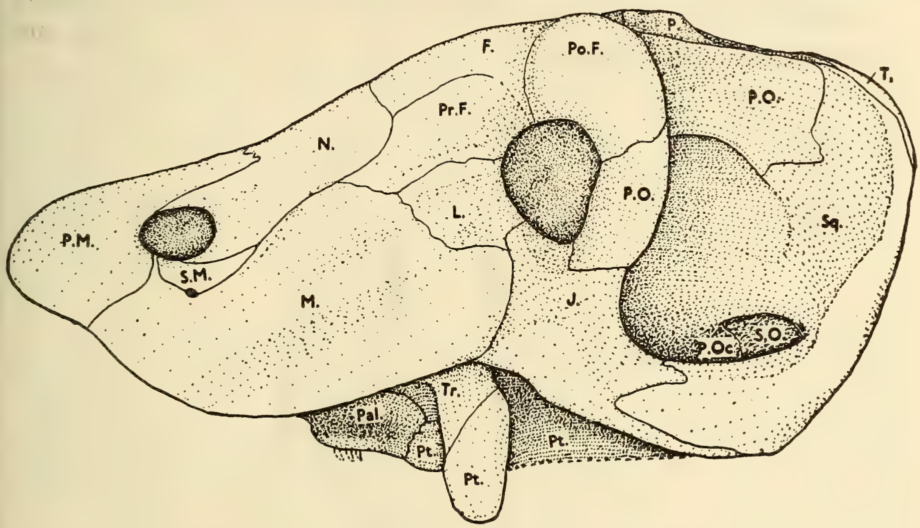


FIG. 8.—*Anteosaurus vorsteri*. Referred specimen. S.A.M. 11577, Bulwater, Beaufort West. Lateral view. ($\times \frac{1}{6}$.)

cross-sections of 7 fairly regular postcanines are seen and on the right 6.

This specimen is of some historical interest in that it was known by the local people to have been exposed when Seeley collected the well-known Tamboerfontein specimen of *Bradysaurus baini*. Weathering is thus not very rapid in the *Tapinocephalus*-zone of the Koup.

Anteosaurus abeli (Boonstra). (Figs. 1, 2, 5, 6, 7.)

Boonstra, L. D. 1952. *Anteosaurus abeli* (Boonstra).

Boonstra, L. D. 1953. *Anteosaurus abeli* (Boonstra).

Holotype. A good skull and lower jaw. S.A.M. 11296. Kruisrivier, Sutherland. Coll. Boonstra.

Skull large, maximum length 700 mm. Snout long, high, moderately wide. Intersquamosal width fairly great (450? mm.). Postfrontal boss fairly large and prominent. Jugal boss low, angular boss very strong. Fronto-naso-prefrontal swelling strong, but only slightly overhanging the sides of the skull. Pineal boss low with rounded edge, situated near occipital

edge. Sharp upward inclination of premaxillary edge. The occiput is high, fairly narrow and deeply concave with a fairly great posterior sweep of the temporal arches and the upper part of the temporal fossa roomy antero-posteriorly; the temporal arch rises above the plane of the intertemporal surface. Palate probably long. *Basis cranii* unknown. Condyle unknown. In the type there are in the left upper jaw 3 incisors, 1 canine and probably 7 postcanines; whereas on the right side there are 4 incisors, 1 canine and ? postcanines. In the dentary there are 2 incisors on both sides.

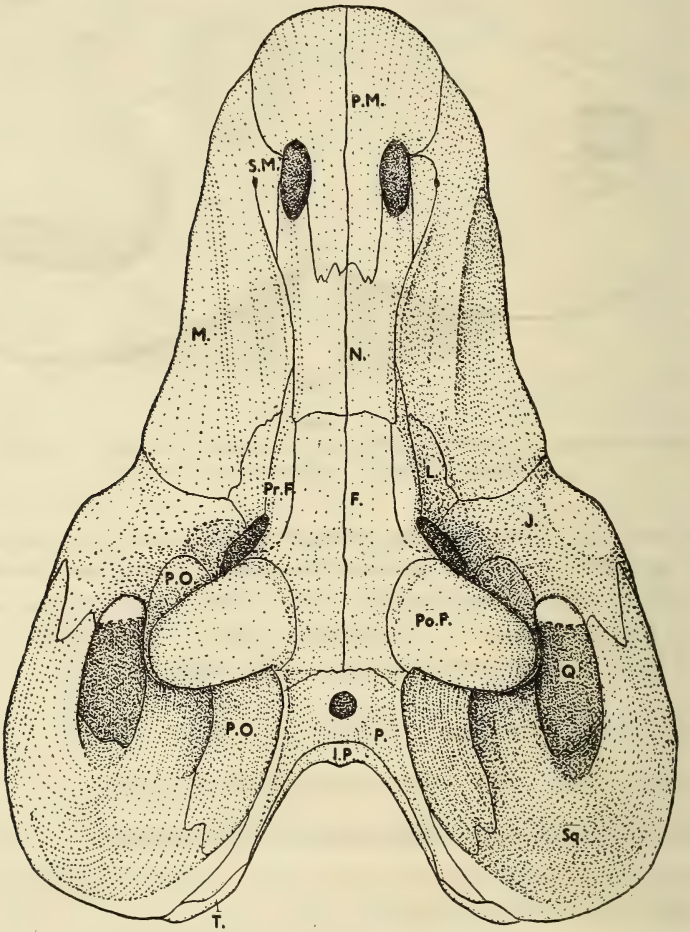


FIG. 9.—*Anteosaurus vorsteri*. Referred specimen. S.A.M. 11577, Bulwater, Beaufort West. Dorsal view. Symmetry restored on the basis of the well preserved left side. (× 1/6.)

Paratype. (Fig. 6.) A good skull and parts of the lower jaw. S.A.M. 4340. Leeurivier, Beaufort West. Coll. Haughton.

I have included this specimen in the species — *abeli* — although it differs from the type in a number of points viz. there is only a faint indication of a jugal boss; the frontal enters the supra-orbital border; the premaxilla has a longer alveolar border and on the left carries 5 incisors — the first 4 being very long and strong whereas no. 5 is small and weak; on the left dentary there are 4 long and strong incisors intermeshing with the upper incisors.

S.A.M. 9123 from Voëlfontein, Prince Albert, consists of the major part of a skull which agrees in all essentials with the type skull. Here there are on the left premaxilla 5 cross-sections of incisor roots; these represent numbers 1-4 with a replacing incisor lying median to no. 4. On the right side cross-sections of nos. 2, 3 and 4 are preserved. On the left there is the root of a large canine, whereas on the right there is the empty alveolus of the canine.

S.A.M. 11576 (Fig. 5) from Klein-Koedoeskop, Beaufort West, consists of the anterior part of both jaws. The upper canines are large strongly curved teeth. On the left premaxilla there are 5 incisors — the first 4 long and strong and the fifth short but strong, whereas on the right there are only the 4 anterior incisors. In both dentaries there are 4 incisors — the first 3 long and strong and the fourth much smaller.

S.A.M. 5621, Leeurivier, Beaufort West, consists of two pieces not in contact, representing most of the dorsal surface of a skull, which closely resembles that of the type skull.

S.A.M. .11949 (Fig. 7), Nuwefontein (Roxana), Fraserburg, consists of a snout and the dorsal part of the posterior part of the skull not in contact. This specimen is weathered beautifully white and in the snout the sutures are very clearly shown and it was in this specimen where I first noticed that the premaxillaries were posteriorly abruptly truncated and not long and tapering as in *Jonkeria* and the Tapinocephalids.

Anteosaurus acutirostris Sp. Nov. (Fig. 10.)

Boonstra, L. D. 1953. *Anteosaurus abeli* (Boonstra) in errore.

Holotype. A good skull and lower jaw. S.A.M. 9329, Kruisvlei, Beaufort West. Coll. Boonstra.

Skull large, maximum length 675 mm. Snout long, high, narrow and light. Intersquamosal width great (480? mm.). Postfrontal boss huge and prominent. Jugal boss massive, angular boss massive. Fronto-naso-prefrontal swelling very strong with a distinct step on to the anterior nasal surface and laterally slightly overhanging the sides of the skull. Pineal boss

low with rounded edges extending to the occipital edge. Fairly strong upward inclination of the premaxillary edge. The occiput is high, fairly wide, very deeply concave with a sharp and great posterior sweep of the temporal arches; upper part of the temporal fossa roomy antero-posteriorly; the temporal arch rises above the plane of the intertemporal surface. Palate apparently long and narrow. *Basis cranii* fairly long. Exoccipitals fused with basioccipital to form a rounded condyle, which is visible beyond the occipital edge in dorsal view. On both sides there are 4 upper and 4 lower incisors, 1 canine and 5? postcanines. In both dentaries there are 4 incisors.

In this specimen the quadratojugal is clearly seen as a small bone resting on a ledge above the outer quadratic condyle as in the Pristerognathid Therocephalians.

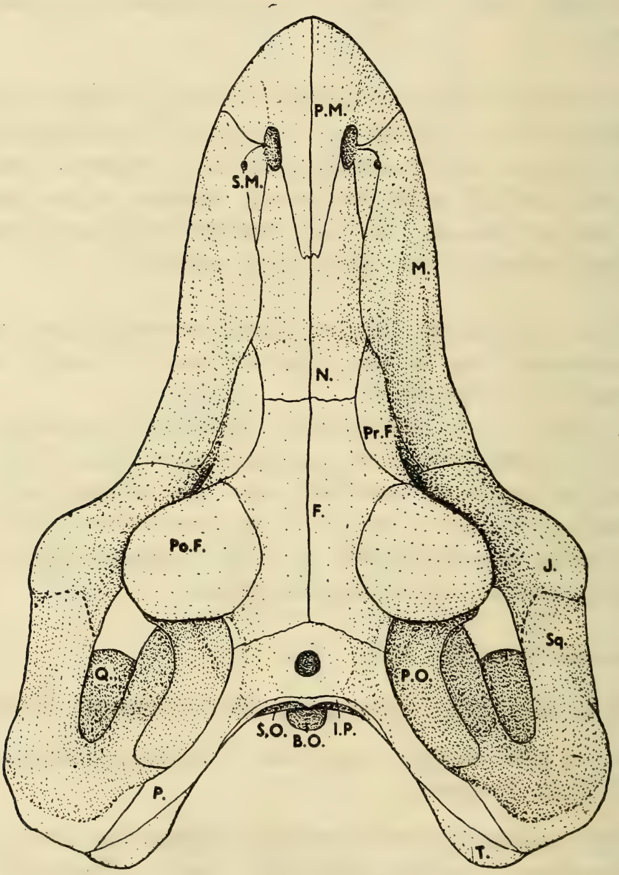


FIG. 10.—*Anteosaurus acutirostris*. Sp. Nov. Holotype. S.A.M. 9329, Kruisvlei, Beaufort West. Dorsal view. Symmetry restored on the basis of the right side, which has suffered a slight side-to-side compression. (× 1/6.)

Associated with the holotype skull of *acutirostris* there were a number of skull fragments of other *Anteosaurus* skulls and in addition a large number of bones of the postcranial skeleton of more than one individual. I hope to be able to describe these bones of the postcranial skeleton in the near future. In the meantime a general statement here will be useful.

As a whole the postcranial skeleton is lightly built without any trace of the massiveness so typical of all the hitherto known South African Deinocephalians. One's first impression is that the skeletal bones could belong to some large Therocephalian — associated, for instance, with a skull not very much larger than that of *Scymnosaurus ferox*. This applies particularly to the femur, which is a long bone with the proximal and distal ends hardly expanded and the shaft long and slender.

Anteosaurus crassifrons Sp. Nov. (Figs. 11, 12, 13-

Holotype. A good skull, but distorted by a simple shear. S.A.M. 11946, Buffelsvlei, Beaufort West. Coll. Boonstra and Marais.

Skull large, but short and quat; maximum length 570 mm. Snout short, high and very wide. Intersquamosal width fairly small (330? mm.). Postfrontal boss fairly massive and prominent. Jugal boss massive, angular boss unknown. Fronto-naso-prefrontal swelling very massive with a very distinct step on to the anterior nasal surface and laterally strongly overhanging the sides of the skull. Pineal boss rounded, large and extending on to the frontal. Very sharp upward inclination of the premaxillary edge. The occiput is high, fairly wide, deeply concave, with a great posterior sweep of

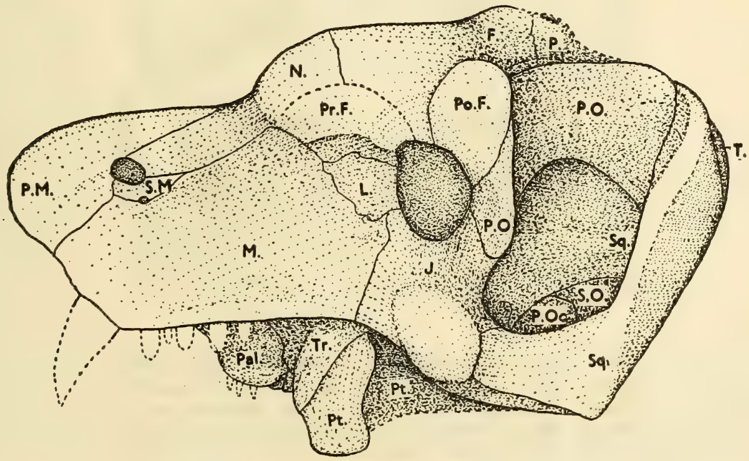


FIG. 11.—*Anteosaurus crassifrons*. Sp. Nov. Holotype. S.A.M. 11946, Buffelsvlei, Beaufort West. Lateral view. (× ⅛.)

the temporal arches, and the upper part of the temporal fossa roomy in antero-posterior direction; the temporal arch not rising above the plane of the intertemporal surface. Palate very short with very massive lateral pterygoidal flanges. *Basis cranii* short, with short basisphenoid. Exoccipitals fused with basioccipital to form a rounded condyle. In both premaxillaries no teeth are preserved but 5 matrix-filled alveoli are shown; in both maxillaries 5 postcanine roots of greatly varying diameter are preserved, numbers 2 and 5 being much smaller than the other 3.

S.A.M. 11302 from Buffelsvlei, Beaufort West, is a fairly complete but weathered skull. Although a somewhat larger skull than that of the type, it clearly belongs to the same species. It has the same massive fronto-naso-prefrontal swelling with a distinct step anteriorly and laterally

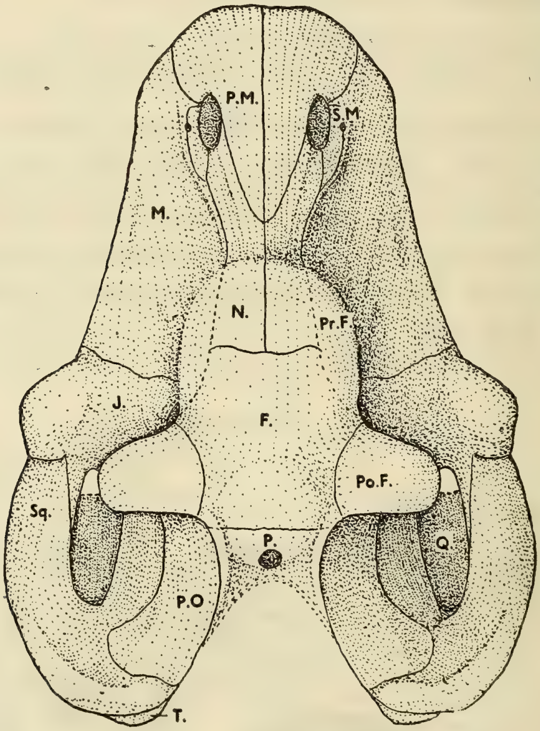


FIG. 12.—*Anteosaurus crassifrons*. Sp. Nov. Holotype. S.A.M. 11946, Buffelsvlei, Beaufort West. Dorsal View. Symmetry affected by a simple shear, restored on the basis of the least affected left side. (× 1/6.)

overhanging the preorbital side-wall; the jugal boss is very massive. On the right side there are stumps of 4 incisors and five or six postcanines; a well

preserved crown of a postcanine is of fair size (25 x 14 x 8 mm.); it is a bluntly conical tooth, labio-lingually compressed.

S.A.M. 11929 from an unknown locality, probably near Abrahamskraal, Prince Albert, is an imperfect, weathered skull in extremely intractable matrix, but showing a fairly good ventral surface. The quadrate shows its articular condyles to lie obliquely in the skull with the outer one the more posterior one as shown in reconstruction in all the figures in this paper, and

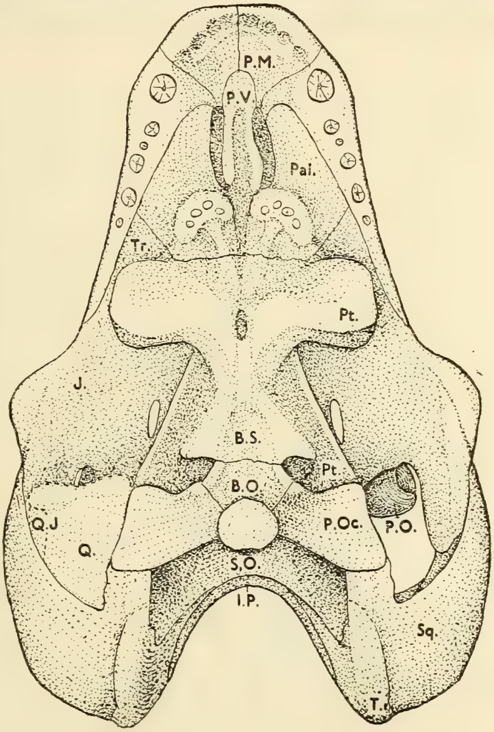


FIG. 13.—*Anteosaurus crassifrons*. Sp. Nov. Holotype. S.A.M. 11946, Buffelsvlei, Beaufort West. Ventral view. Symmetry restored on the basis of the left half of the palate with the result that it is narrower than it would have been in life. On the right the quadrate-complex is indicated in position. ($\times \frac{1}{8}$.)

thus not as shown in Broom's figure of *Anteosaurus vorsteri*. Part of the left stapes can also be seen and this bone appears to be stout, firmly wedged in the *fenestra ovalis* and abutting against the medial edge of the quadrate dorsal to the extremity of the quadrate ramus of the pterygoid, which appears to overlap the postero-median surface of the quadrate as in *Jonkeria* and the Tapinocephalids. The *basis cranii* is short and wide, with a short basisphenoid. The roots of five postcanines are preserved in the right maxilla.

Anteosaurus major Sp. Nov. (Figs. 14, 15)

Boonstra, L. D. *Anteosaurus abeli* (Boonstra) in errore.

Holotype. A good skull, lacking the snout, but somewhat dorso-ventrally compressed. S.A.M. 11293. Boesmansrivier, Beaufort West. Coll. Boonstra.

Skull very large, maximum length 805? mm. Snout long, fairly broad and high. Intersquamosal width very great (612 mm.). Postfrontal boss

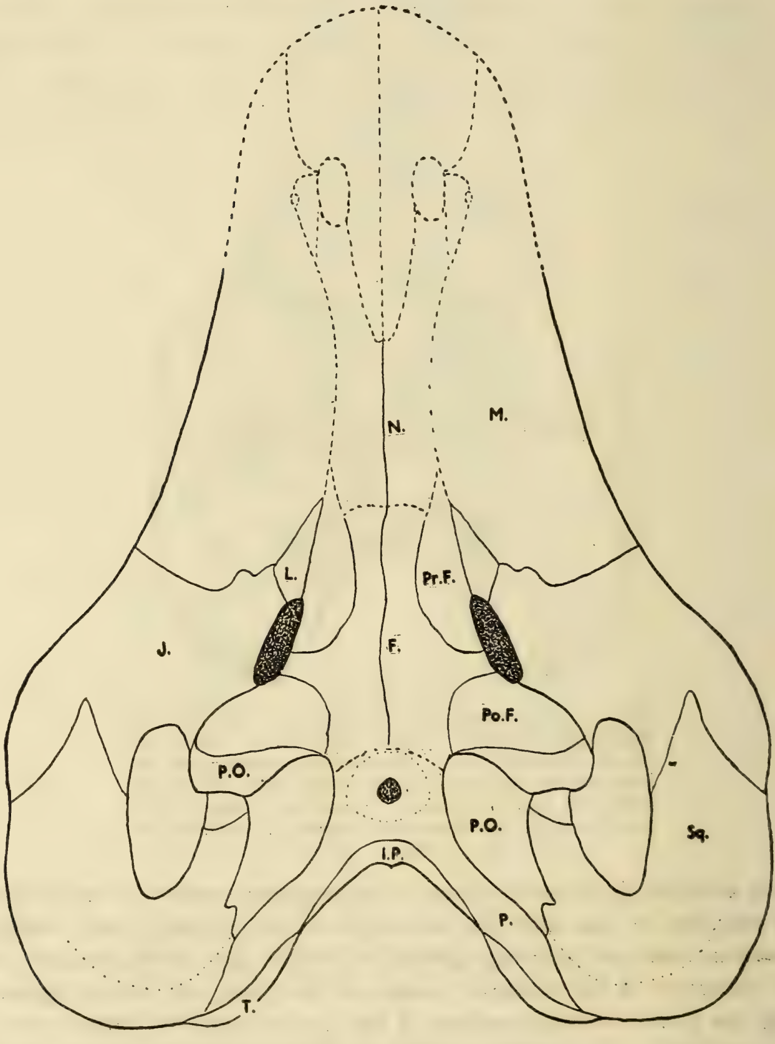


FIG. 14.—*Anteosaurus major.* Sp. Nov. Holotype. S.A.M. 11293, Boesmansrivier, Beaufort West. Dorsal view. Symmetry disturbed by dorso-ventral crushing restored on the basis of the left side. (× ⅙.)

only moderately strong and not very prominent, with postorbital forming the postero-lateral part. Low and weak jugal boss, angular boss unknown. Fronto-naso-prefrontal boss moderate, confluent with anterior nasal surface. Pineal boss low, with rounded edges, situated some distance from the occipital edge. Premaxilla unknown. The occiput is low and broad, moderately deeply concave, sweep of temporal arches more laterally than posteriorly and the upper part of the temporal fossa roomy antero-posteriorly; the temporal arch rising above the level of the intertemporal surface. Palate fairly long

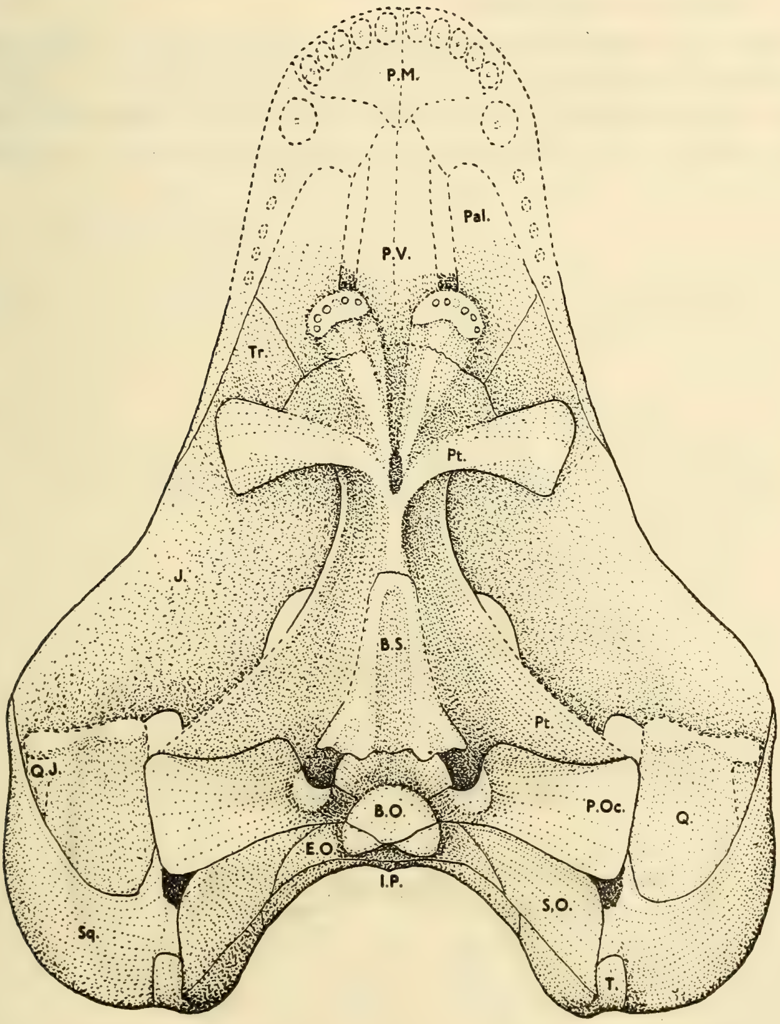


FIG. 15.—*Anteosaurus major*. Sp. Nov. Holotype. S.A.M. 11293, Boesmansrivier, Beaufort West. Ventral view. Symmetry restored on the basis of the left side, which is least disturbed. (× ⅛.)

and broad, with strong and deep lateral pterygoidal flanges but not so massive as in *crassifrons*. *Basis cranii* long and basisphenoid much longer than in any of the other species. Exoccipitals forming the dorso-lateral corners of the condyle. No teeth are preserved.

Anteosaurus laticeps Sp. Nov. (Figs. 4, 16)

Holotype. An incomplete skull showing only the ventral and most of the occipital surface. S.A.M. 11592. Dikbome, Laingsburg. Coll. Boonstra and Du Plessis.

Skull large, maximum length 645? mm. Snout short and very broad. Intersquamosal width great (522 mm.). Postfrontal boss unknown. Jugal and angular bosses unknown. Fronto-naso-prefrontal region unknown. Pineal region unknown. Premaxilla unknown. The occiput is low and very broad,

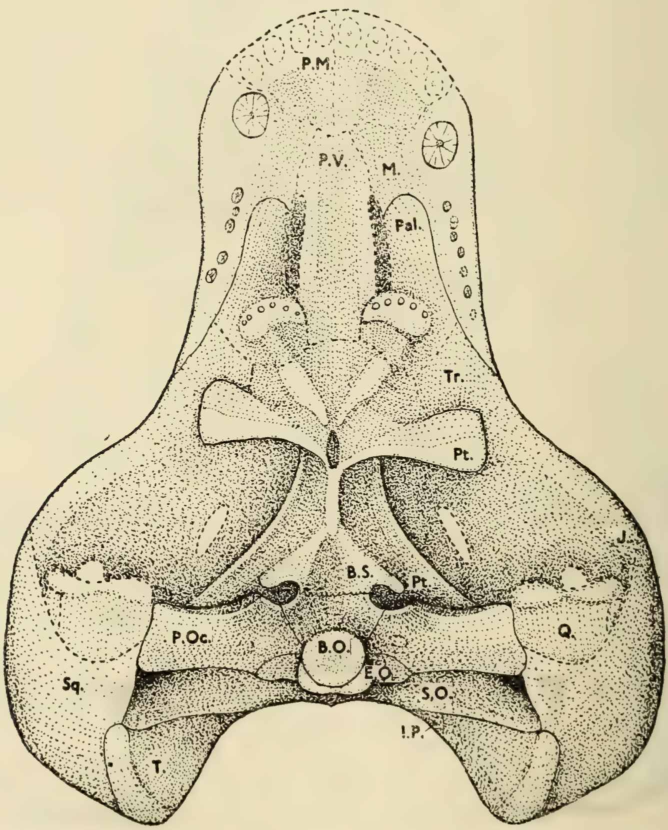


FIG. 16.—*Anteosaurus laticeps*. Sp. Nov. Holotype. S.A.M. 11592, Dikbome, Laingsburg. Ventral view based mainly on the right side. (× ⅛.)

shallowly concave; sweep of temporal arches mostly laterally. Palate long and very broad with only moderately strong lateral pterygoidal flanges. *Basis cranii* short, with very short basisphenoid. Exoccipitals forming much of the dorso-lateral corners of the condyle. No incisors are preserved, the canines are very strong, slightly recurved teeth; in the right maxilla stumps of five postcanines can be made out, whereas on the left five teeth are preserved with the probability of another two making a total of 7. The postcanines are bluntly conical, but linguo-labially compressed teeth with the crowns thus oval in crosssection (16 x 11 x 7 mm.).

Anteosaurus cruentus Sp. Nov. (Figs. 17, 18, 19, 20)

Boonstra, L. D. 1953. *Anteosaurus minor* (Broom) in errore.

Holotype. A good, undistorted skull, but lacking the lower jaw. S.A.M. 11694, Koringplaas, Moordenaarskaroo, Laingsburg. Coll. Boonstra and Du Plessis.

Skull moderately large, maximum length 565 mm. Snout long, narrow and fairly low. Intersquamosal width not great (360 mm.). Postfrontal boss

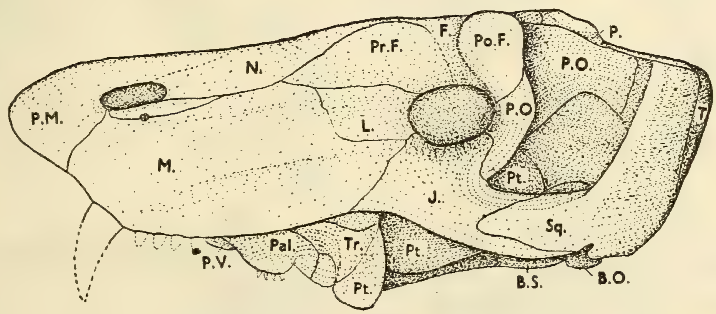


FIG. 17.—*Anteosaurus cruentus*. Sp. Nov. Holotype. S.A.M. 11694, Koringplaas, Laingsburg. Lateral view with the quadrate-complex missing. (× ⅙.)

fairly strong and prominent. No jugal boss, angular boss unknown. Fronto-naso-prefrontal swelling small, passing evenly on to the anterior nasal surface. Pineal boss prominent, with sharp circular border, situated very near the occipital edge. Sharp upward inclination of the premaxillary edge. The occiput is high and fairly broad, very deeply concave with a great posterior sweep of the temporal arch and the upper part of the temporal fossa roomy antereo-posteriorly; the temporal arch not rising above the very

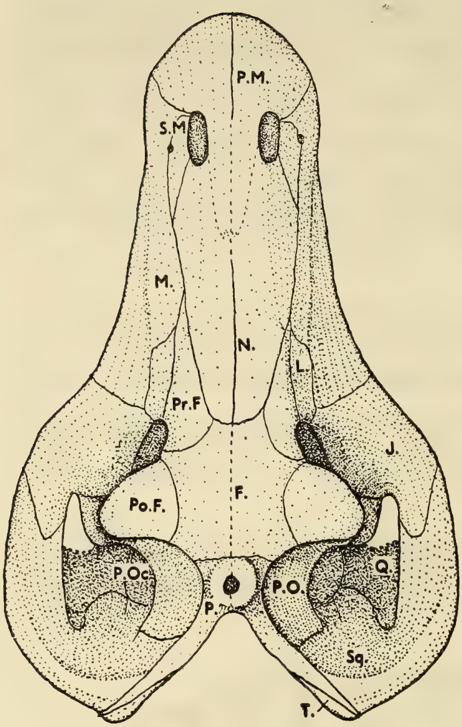


FIG. 18.—*Anteosaurus cruentus*. S. Nov. Holotype. S.A.M. 11694, Koringplaas, Laingsburg. Dorsal view. (× 1/6.)

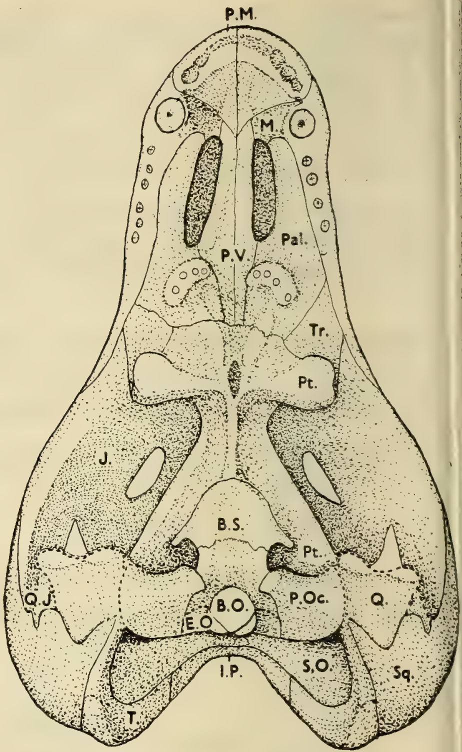


FIG. 19.—*Anteosaurus cruentus*. Sp. Nov. Holotype. S.A.M. 11694, Koringplaas, Laingsburg. Ventral view. (× 1/6.)

narrow intertemporal surface. Palate long, with fairly robust lateral pterygoidal flanges. *Basis cranii* long, but the basisphenoid is short. The exoccipitals forming a large part of the dorsolateral corners of the condyle. No trace of incisors is preserved; the alveolar face of the premaxillaries shows a matrix filled groove divided in its posterior part into distinct adveoli; there appears to be room for 5 incisors when developed. On the right the canine root is followed by roots of 6 postcanines, but on the left only four roots with a possible fifth can be seen.

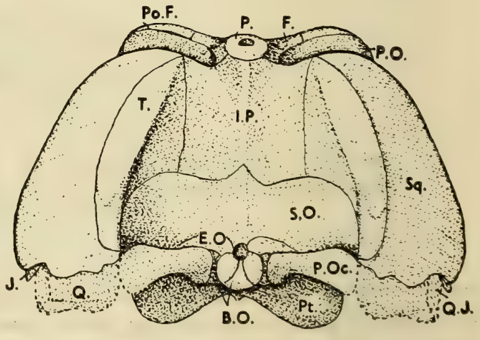


FIG. 20.—*Anteosaurus cruentus*. Sp. Nov. Holotype. S.A.M. 11694, Koringplaas, Laingsburg. Occipital view. (× 1/6.)

S.A.M. 9140 from Voëlfontein, Prince Albert, is an imperfect disarticulated skull agreeing fairly well with the type, but is of some interest in that it shows a number of the roofbones as separate elements with exposed sutural faces.

Anteosaurus levops Sp. Nov. (Fig. 21)

Holotype. A weathered skull, without the lower jaw. S.A.M. 11492. Mynhardtskraal, Beaufort West. Coll. Boonstra.

Skull fairly small, maximum length 485 mm. Snout fairly short, lightly built, narrow and low. Intersquamosal width relatively large (415 mm.). Postfrontal boss strong and prominent. No jugal boss; angular boss unknown. Fronto-naso-prefrontal swelling strong with a distinct step onto the anterior nasal surface and laterally slightly overhanging the sides of the skull. Pineal boss apparently prominent, reaching the occipital edge. Upward inclination

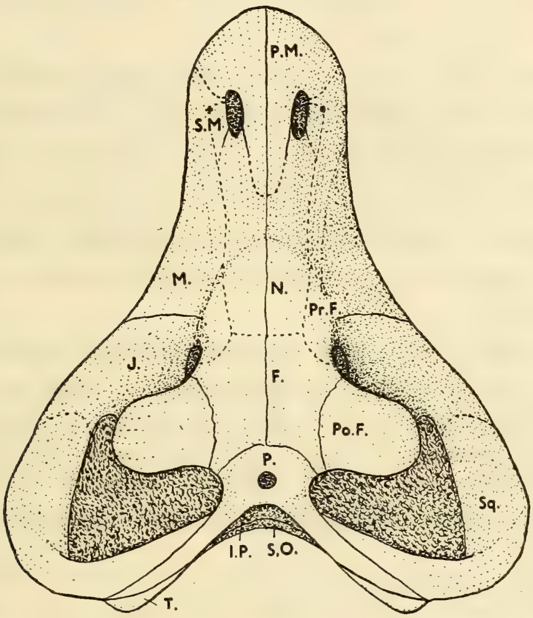


FIG. 21.—*Anteosaurus levops*. Sp. Nov. Holotype. S.A.M. 11492, Mynhardtskraal, Beaufort West. Dorsal view. Temporal fossae not cleared of matrix. ($\times \frac{1}{6}$.)

of the premaxillary edge moderate. The occiput is fairly low and broad; deeply concave, not vertical; strong postero-lateral sweep of the temporal arches and the upper part of the temporal fossa shortened in antero-posterior direction; the temporal arch rising above the plane of the narrow intertemporal

surface. Palate long and narrow. *Basis cranii* fairly short. Condyle unknown. In the right premaxilla parts of the crowns of 3 incisors are preserved, but on the left there is a matrix filled groove with no sign of any teeth.

Anteosaurus minusculus Sp. Nov.

Boonstra, L. D. 1936. *Anteosaurus minor* (Broom) in errore.

Holotype. A distorted skull with the greater part of the arches and most of the palate missing.

American Museum of Natural History, No. 2224. Vanderbylskraal?, Beaufort West. Coll. Broom.

This specimen in the American Museum is stated by Broom to be the topotype of the skull fragment in the British Museum (Natural History) R.5742.

In my paper on the Titanosuchids in the American Museum I attempted a reconstruction of the dorsal aspect of the skull and showed the premaxilla as a long posteriorly tapering bone. With our present knowledge of the truncated posterior end of the premaxilla in all species of *Anteousaurus* this was obviously an error in observation. As this skull has well developed postfrontal bosses it cannot belong to *Pseudanteosaurus minor* (Broom) and I propose to regard it as a new species of *Anteosaurus* under the specific name — *minusculus* sp. nov.

The skull is fairly small with a maximum length of 480 mm.; the snout is long, broad and fairly high; the intersquamosal width was probably small (225? mm.); the postfrontal boss quite strong and prominent; there is no jugal boss; the fronto-naso-prefrontal swelling is weak; the occiput is vertical, very deeply concave with a great posterior sweep of the temporal arches and the upper part of the temporal fossa is roomy in antero-posterior direction.

Anteosaurus sp. (Fig. 22)

S.A.M. 2752, Viviers Siding, Beaufort West. Coll. Haughton and Whaits.

In this specimen we have only the posterior two thirds of the upper surface of a skull. Although it cannot be included in any of the above described species I am not naming it. The skull differs from all the described forms in that the prominent mound-like pineal boss overhangs the occipital surface; the occiput is very deeply concave from side to side with the two horns of the parietal directed nearly wholly in posterior direction; in the posterior

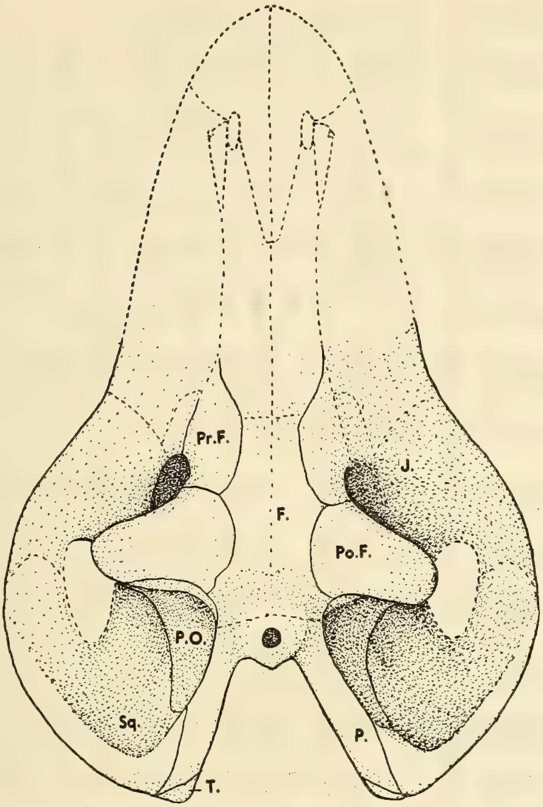


FIG. 22.—*Anteosaurus sp.* S.A.M. 2752, Viviers Siding, Beaufort West. Dorsal View. (× ⅛.)

part of the frontals there is a step bringing this part of the surface down to a lower level than that of the anterior part of the frontals. The postorbitals form a small part of the posterior surface of the boss, whose surface is in other species wholly formed by the postfrontal. These bosses are only moderately strong and prominent. There is very little swelling in the fronto-naso-prefrontal region, but notwithstanding this the prefrontal is so developed to exclude the frontal from entering the supraorbital border.

Discussion

From the above account it is clear that *Anteosaurus* is a genus of the Deinocephalia quite distinct from all the known South African genera. It may be characterised as follows: skull large, with prominent postfrontal bosses; temporal fossa with large dorso-ventral diameter and deep antero-ventral bay; infratemporal bar narrow; quadratojugal no longer lying

CHIEF MEASUREMENTS IN MM.

	A. magnificus B.M.N.H. R 3595	*A. lotzi* A.K. ?	*A. vorsteri* T.M. 265	*A. vorsteri* S.A.M. 11577	*A. abeli* S.A.M. 11296	*A. abeli* S.A.M. 4340	*A. abeli* S.A.M. 5621	*A. abeli* S.A.M. 9123	*A. crassifrons* S.A.M. 11946	*A. crassifrons* S.A.M. 11302	*A. crassifrons* S.A.M. 11929	*A. acutirostris* S.A.M. 9329	*A. major* S.A.M. 11293	*A. laticeps* S.A.M. 11592	*A. cruentus* S.A.M. 11694	*A. levops* S.A.M. 11492	*A. minusculus* A.M.N.H. 2224
P.M.—Tab.	660?	750?	740	720	700	680	—	—	570	625	525?	675	805?	645?	565	483	480
P.M.—I.P.	570?	—	581?	600	612	540?	525?	530	460?	535	480?	550	675?	546?	471	396	414
P.M.—Orbit	385?	480?	400?	396	408	363	330?	340	310	340	—	354	465	—	321	270	276
Pin. For.—I.P.	25	—	35?	39	33	—	—	—	—	30	—	30	51	—	15	14	24
Max. Width over Sqs.	360	—	600	528	450	450	—	—	330	330	400?	480	612	522	360	414	222?
Interorbital Width	150	—	145?	120	130	115	135	125	144	147	150	150	132	—	105	108	84
Intertemporal Width	102	—	175?	96	90	—	—	—	81	90	75?	120	87	—	48	69	60
Width over Po. F. bosses	306	—	217?	309	265	275	293	280	270	250	300	291	309	—	210	246	192
Width of snout over Nares	204	136	210?	225	205	200	—	183	210	170	—	171	—	216	141	123	132?
P.M.—B.O.	—	—	636	561?	—	—	—	—	435	—	450?	354	665?	531?	330	—	—
P.M.—Post edge of Lat. Pt. Flange	—	—	385?	360	—	—	—	—	273	—	250?	—	390	354?	303	260?	—
Length of B.S.	—	—	70?	—	—	—	—	—	80?	—	60	—	147	51	50	—	—
Width over Lat. Pt. Flanges	—	—	250?	240	—	—	—	—	210	—	220	—	285	228	162	165?	—

In the case of the forms described by other authors I have included the measurements given by them augumented by measurements taken from their published figures.

on the surface on the latero-postero-ventral corner of the skull but shifted medially as in the higher Therapsids; alveolar border of the premaxilla inclined upwards to give working space to the long, simple, pointed incisors; a short series of postcanine teeth, rather small and irregular; deeply concave occiput; ridge forming the outer border of the occiput proper formed solely by the tabular and squamosal; postorbital covering the lateral face of the parietal and with a long contact with the squamosal; fronto-naso-prefrontal region swollen to a greater or lesser extent; with bosses on the jugal and angular in the larger species; number of incisors variable; great posterior overlap of the maxilla over the jugal.

If the Titanosachia are defined as Deinocephalians with a carnivorous dentition, with quadrate not displaced far anteriorly, with concave occiput, with spacious temporal fossa, then *Anteosaurus* is undoubtedly a Titanosuchian.

The only other S.A. Titanosuchian genus in which the skull is adequately known is *Jonkeria.*

Anteosaurus differs from *Jonkeria* in a number of important points: in *Anteosaurus* the quadratojugal is no longer a surface bone, but has shifted medially (in one species of *Jonkeria* viz. *vanderbyli,* there is an indication that here also there is a similar tendency); in *Anteosaurus* the infratemporal bar is narrow (again *J. vanderbyli* shows a similar tendency); in *Anteosaurus* the temporal fossa extends far ventrally and has in addition an anterior bay of the fossa extending to under the postorbital bar; the postfrontal develops a large boss in *Anteosaurus,* whereas this bone is a small element in *Jonkeria;* large jugal and angular bosses are unknown in *Jonkeria* and the fronto-naso-prefrontal region remains unswollen; the pineal foramen is situated near the occipital edge in *Anteosaurus,* whereas in *Jonkeria* it is situated in the plane of the postorbital bar; in *Jonkeria* the premaxillary edge does not curve sharply upwards; no reniform palatine boss bearing teeth is known in *Jonkeria;* the lateral pterygoidal flanges are much weaker in *Jonkeria;* in *Jonkeria* the posterior sheet of the postorbital does not cover the whole lateral face of the parietal; in *Jonkeria* the jugal is a much smaller bone and does not flare out laterally as it does so characteristically in *Anteosaurus,* nor does it extend so far posteriorly lying along the inner face of the squamosal; in *Jonkeria* the postcanines form a long series, whereas this is short in *Anteosaurus;* the posterior process of the premaxilla in *Jonkeria,* as in the Tapinocephalians, is much longer than in *Anteosaurus;* in *Jonkeria* the ridge on the occiput is formed by the paroccipital, squamosal and tabular, whereas in *Anteosaurus* the paroccipital does not enter into it at all; in *Anteosaurus* the quadrate rami of the pterygoid curve much outwards as they approach the quadrate, whereas in *Jonkeria* they lie nearly parallel to the median line; in *Anteosaurus* the stapes is a much longer bone; in

Anteosaurus the maxilla has a much greater overlap over the jugal. These differences, together with others not listed here, to my mind show that these two genera lie on lines of development sufficiently divergent to warrant our placing them in different families, which I propose to name the *Anteosauridae* and the *Jonkeridae*.

It is thus clear that the Anteosauridae, although retaining a number of primitive characters, have advanced farther in some points of structure than their contemporaries the Jonkeridae.

Comparison with Other Therapsids

In South Africa the Therapsids are first encountered in the *Tapinocephalus-zone*. With its complex of monoclinal folds it has up to the present not been possible to establish from what level within the zone the various known Therapsid finds have come. Until then we are forced to consider the assemblage of forms from this zone as being contemporaneous.

The thus contemporary Therapsids from the *Tapinocephalus*-zone are: Anningiamorpha, Dromasauria, Anomodontia, Gorgonopsia, Therocephalia and Deinocephalia. These are all present as well established groups clearly distinct from each other.

The Anningiamorphs are not very well known, but appear to be a group in which a large number of primitive characters have persisted.

The Dromasaurians are only known from four specimens and combine a number of primitive characters with some rather specialised.

The Anomodonts, although but poorly represented in this zone compared to the great diversity developed in the younger rocks of the Karroo, are already quite specialised when they are first encountered. No group with such a remarkable edentulous premaxilla can be anything but firmly set on an independent line of development.

The Gorgonopsians, with but a few forms present in the *Tapinocephalus*-zone, blossomed exceedingly in later ages, but the oldest known species are already definite Gorgonopsians with a habitus well established and clearly their own and the subsequent developments in no way exceeded the limitations inherent in these early forms from the *Tapinocephalus*-zone.

The Therocephalians of the *Tapinocephalus*-zone are a virile suborder of the Therapsids already represented by a large number of species, which, representing different lines of development, can be placed in a number of different families. Having already, by the beginning of the *Tapinocephalus*-zone times, split into a number of families it is clear that the tempo of development within the suborder during the antecedent ages must have been greater than in the Gorgonopsians. This was probably due to a greater lability in the original stock. As their successors — not only the higher Therocephalian families but also their off-spring the Cynodonts, Bauriamorphs

and Ictidosaurians, of the later Karroo Beds — show, this lability or greater potentiality for further development beyond the confines of the suborder was maintained.

The Deinocephalians, when first encountered in the *Tapinocephalus*-zone, were already at the end of their tether. They are represented by the end-products of their particular line of development which culminated in the 3 specialised groups — Titanosuchia, Tapinocephalia and Styracocephalia.

Characters of a Postulated Primitive Therapsid Ancestor

If we postulate a primitive Therapsid ancestor, common to all the Therapsids, situated on a morphological level somewhere between that of the early Pelycosaurs and the first Therapsids we would expect it to have the following characters: intertemporal region broad and flat; preparietal absent; premaxilla without long posterior process intercalated between the nasals; the postfrontal well developed; the postorbital covering the lateral face of the parietal and meeting the squamosal; the pineal foramen well in advance of the occipital edge i.e. the upper occipital edge has not yet migrated anteriorly; the premaxilla below the nostril would still be shallow; the zygomatic arch shallow; the temporal fossa relatively small with the squamosal not bowing out laterally or posteriorly; the quadratojugal still lying on the outer surface i.e. not yet migrated internal to the squamosal; the occiput low, fairly narrow, vertical, with its upper border not moved anteriorly, not deeply concave from side to side; the paroccipital just beginning to strengthen and to support the quadrate; the quadrate would still be large with its condyle lying fairly far ventrally, but still in the posterior position i.e. in line with the occipital condyle; the premaxilla would be dentigerous and with hardly any palatal face; the maxillary teeth would form a long series and there would probably already be a specialised canine; choanae and nares anteriorly situated; no suborbital opening; the lateral pterygoidal processes would still be situated fairly far back and be fairly weak; the basisphenoid-pterygoid joint would no longer be movable and the contact of the basisphenoid with the pterygoid shifted posteriorly; the basisphenoid processes flattening; the quadrate ramus of the pterygoid reduced in height; the parasphenoidal rostrum would still be visible in the posterior part of the interpterygoidal slit; there would be no coronoid process to the dentary; the lower jaw long and the angular notch and reflected lamina would be beginning to develop.

Tabulating the characters of the Therapsids of the *Tapinocephalus*-zone on the basis of the above list one gets the following result:

The Anningiamorpha are not sufficiently well known to make a count of the characters corresponding with those in the above list, but those preserved

point to this group as approaching the postulated primitive Therapsid condition most closely.

The Dromasauria, as far as they are known, appear to occupy the second place.

Then come the three groups of the Deinocephalia — which, although clearly distinct from each other — due to particular specialisation — seem to stand on more or less the same morphological level.

Somewhat further removed from the postulated primitive Therapsid condition are the Dicynodonts, and then come the Gorgonopsians, followed by the Therocephalians in which the rate of development away from the primitive Therapsid condition has been the greatest.

Finally, *Anteosaurus* has advanced beyond the primitive Therapsid stage in the following characters: the premaxilla, below the nostril has increased in depth and then the alveolar edge has curved upwards; the temporal fossa has become very roomy and the squamosal is bowed out strongly both laterally and posteriorly; the quadratojugal has migrated from the outer surface to lie medial of the zygoma; the occiput has greatly increased its surface by becoming both broad and high; the paroccipital process has become very strong and supports the quadrate firmly; the length of the postcanine series has decreased and the long incisors have become intermeshing teeth; the lateral pterygoidal processes are situated well forward and are very strongly developed; the basisphenoid-pterygoid region has advanced as in higher Therapsids, but there are no strong basisphenoidal tubera and lastly we have the characteristic pachyostosis with the development of the peculiar postfrontal, jugal and angular bosses.

REFERENCES

Boonstra, L. D. 1936. The Cranial Morphology of Some Titanosuchid Deinocephalians. Bull. Am. Mus. Nat. Hist. 72, 3, 99-116.

Boonstra, L. D. 1948. Miljoene Jare Gelede in die Karoo. Voortrekkerpers, Johannesburg.

Boonstra, L. D. 1952. 'n Nuwe *Titanosuchiërsoort* (*Anteosaurus abeli*). Tydskrif vir Wetenskap en Kuns. 12, 1, 150-151.

Boonstra, L. D. 1953. A Suggested Clarification of the Taxonomic Status of the South African Titanosuchians. Ann. S. Afr. Mus. 42, 1, 19-28.

Broili, F. and Schröder, J. 1935. Ein Dinocephalen-Rest aus den unteren Beaufort-Schichten. Sitzb. Bay. Akad. Wiss. Sonderdruck. 93-114.

Broom, R. 1910. Observations on some Specimens of South African Fossil Reptiles preserved in the British Museum. Trans. Roy. Soc. S. Afr. 2, 1, 19-25.

Broom, R. 1929. On the Carnivorous Mammal-like Reptiles of the Family Titanosuchidae. Ann. Trans. Mus. 13, 1, 9-36.

Broom, R. 1936. On some New Genera and Species of Karroo Fossil Reptiles, with Notes on some others. Ann. Trans. Mus. 18, 4, 349-386.

Broom, R. 1936. On the Structure of the Skull in a New Type of Deinocephalian Reptile. Proc. Zool. Soc. 733-742.

Watson, D. M. S. 1914. The Deinocephalia, an Order of Mammal-like Reptiles Proc. Zool. Soc. 749-786.

Watson, D. M. S. 1921. The Basis of Classification of the Theriodontia. Proc. Zool. Soc. 35-98.

9. *The Smallest Titanosuchid yet recovered from the Karroo.* By L. D. Boonstra, D.Sc.

(With Plate XVIII and 5 text-figures)

In the collection of the South African Museum there is a specimen (S.A.M. 4323) collected by Haughton on the Merweville Commonage in 1917. This had been entered in the register as a Gorgonopsian, presumably because of its small size. The specimen as preserved consists of the anterior third of a small skull, the major part of a manus, a tarsus, a nearly complete femur, a radius, a fibula, part of the head of the humerus, a coracoid, a series of caudal vertebrae and some other fragments. This is the first specimen of a South African Deinocephalian in which most of the bones of the fore- and hindfoot have been found in articulation.

The Skull (fig. 1)

In the accompanying figure the lateral aspect of the snout is given, with the missing part of the skull indicated by broken lines. The snout is very similar in general build to that known in the large *Anteosaurus,* although in size it is less than $\frac{1}{3}$ of *Anteosaurus abeli*. The nostril is not terminal; the alveolar border, anterior to the canine, sweeps sharply upwards; this reduction of the premaxilla creates the space necessary for the large anteriorly directed anterior incisors, whose function has become that of snatching, piercing and tearing teeth (cf. mechanical grab); the five upper incisors, increasing rapidly

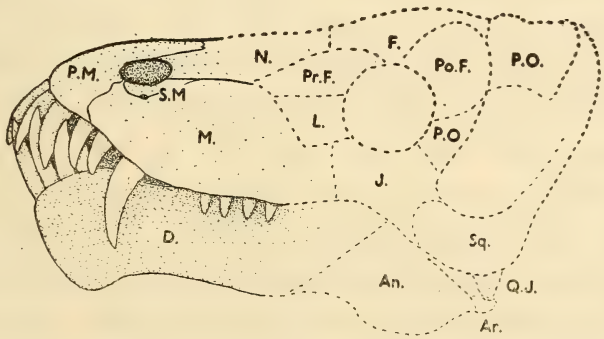


Fig. 1.—*Micranteosaurus parvus* Gen. et Sp. Nov. Lateral view of anterior third of the skull with the missing posterior two thirds in broken lines based on the structure of *Anteosaurus*. S.A.M. 4323. Commonage, Merweville, Beaufort West District. ($\times \frac{1}{3}$.)

in size from number 5 to number 1, intermesh with the four incisors of the dentary; the lower incisors also increase rapidly in size from number 4 to number 1, but they are directed upwards and very much less anteriorly than are the upper incisors; the posterior border of the incisors forms a sharp cutting edge with fairly fine serrations; the upper incisors occupy 55 mm. on the left and 57 mm. on the right side (measured over the curve).

Between the last incisor and the canine there is a diastema of 5 mm. on the left and 4 mm. on the right side. The canine is a strong curved tooth with a length of 35 mm. and at the base of the crown the antero-posterior diameter is 14 mm.; its posterior edge, though sharp, is not serrated.

Between the canine and the first postcanine there is a diastema of 27 mm. on the left and 23 mm. on the right side; on the right the first and second postcanines are in part preserved, whereas on the left the first, third and fourth are in part preserved; the postcanines are small stubby teeth apparently irregularly spaced and functionally unimportant.

The dentary is strong with the alveolar border housing the incisors bent downwards to increase the space necessary for the very long anterior incisors; the symphysis is strong; the mentum squarish with ventrally a "gonial" or "digastric" tubercle.

The premaxilla extends some distance posteriorly between the nasals. The limits of the septomaxilla are not very clear, but the bone is small and apparently forms the ventral border of the nostril as shown in the figure. The maxilla is not swollen above the canine so that it would appear that the root of the canine is not strong. Anteriorly the maxilla has a large overlap over the premaxilla.

Femur (fig. *2a*)

Except for its distal end the femur is fairly well preserved. It is a long slender bone with both its proximal and distal end unexpanded and the shaft long and slender. A twist in the shaft places the distal end at right angles to the proximal end. The proximal facet is directed appreciably anteriorly. No external trochanter is differentiated on the posterior edge of the bone and the area for the insertion of the ilio-femoralis is narrow. Anteriorly a ridge separates this area from the area for the insertion of the pubo-ischio-femoralis internus. The posterior condyle has no epicondylar widening and the facet for the fibula is terminal. The intercondylar fossa is shallow and so is the popliteal fossa. The intertrochanteric fossa is shallow, and with no clearly differentiated external and internal trochanters developed, it is not clearly demarcated either anteriorly or posteriorly. There is thus little left of the primitive Y ridges.

It is thus evident that this femur differs greatly from that hitherto described in any South African Deinocephalian where the bone is usually a short stout

element with short wide shaft and greatly expanded distal and proximal ends. Although superficially resembling the femur of Therocephalians and Gorgonopsians, it differs strikingly in the absence of a differentiated external trochanter and in the rotation of the ends on the shaft.

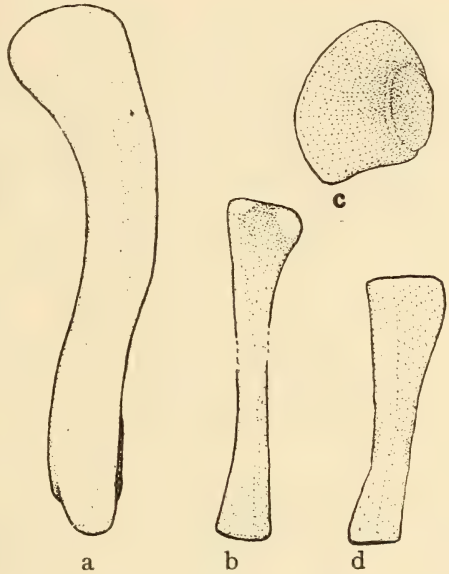


FIG. 2.—*Micranteosaurus parvus* Gen. et Sp. Nov. S.A.M. 4323, Commonage, Merweville, Beaufort West District. *a*, Dorsal view of left femur. ($\times \frac{1}{3}$.) *b*, Ventral view of fibula. ($\times \frac{1}{3}$.) *c*, Dorsal view of left coracoid. ($\times \frac{1}{3}$.) *d*, Dorsal view of radius. ($\times \frac{1}{3}$.)

FIBULA (fig. 2*b*)

The fibula is a lightly built long and slender bone with its proximal end strongly expanded and with its articulating facet for the femur terminal. Whereas the proximal end is flattened, the distal facet is broadly oval in outline.

PES. (plate XVIII*a* and fig. 3)

When this specimen came under my notice it had already been partly cleared of matrix and the parts glued together. Before preparing it further I embedded the whole in plaster. In the accompanying plate I give a photograph of the pes after preparation and still in the plaster bed. From this it is evident that the two proximal tarsals joined by matrix were rotated as a unit through 180° when joined by glue to the distal part of the pes in

the original preparation. In Fig. 3 the proximal tarsal elements are shown right side up.

The intermedium is an ovoid bone with its outer border concave and facing a similar concavity of the fibulare, thus creating a passage for an artery.

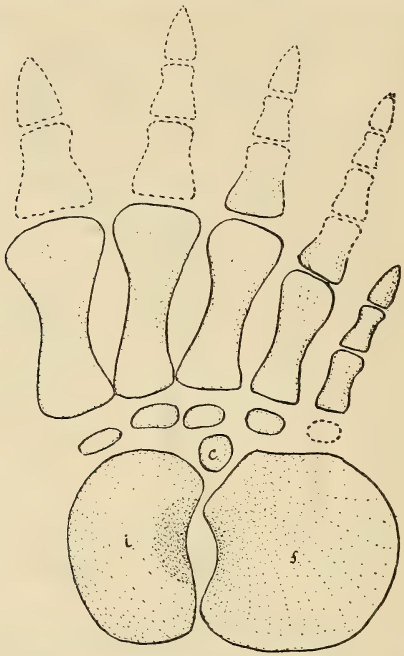


FIG. 3.—*Micranteosaurus parvus* Gen. et Sp. Nov. S.A.M. 4323, Commonage, Merweville, Beaufort West District. Semi-diagrammatic restoration of the right pes seen in dorsal view × about $\frac{3}{4}$. C—centrale; F—fibulare; I—intermedium.

The fibulare is a dorso-ventrally flattened bone, but thickened both proximally and distally to form articulating facets for the fibula and centrale and 4th distale respectively.

The single centrale is a small pebble-like bone.

Four distalia are preserved, but a fifth must also have been present.

Five metacarpals are preserved as shown in the illustrations; they are dorso-ventrally flattened bones, constricted in the waist and with their distal ends more expanded than the proximal ends. No. 1 differs but little from No. 2, but the 4th and especially the 5th are much reduced.

Phalanges. In the first two digits no phalanges are preserved, and in the 3rd and 4th only the proximal end of the first phalanges are present; in the little toe there is a fairly long phalanx and an ungual phalanx preserved.

The tarsal formula is thus 2, 1, 5, and the phalangeal formula 2?, 3?, 3?, 4?, 2.

The pes is thus still closely related to that of the Pelycosaurians.

CORACOID (fig. 2*c*)

The left coracoid is preserved. It is roughly circular in outline; thickened laterally where it carries an articular facet to form the lower part of the glenoid articulation; medially it forms a fairly thin sheet of bone with a concave upper and a convex under surface. Anteriorly it has a free edge and is not suturally united to the procoracoid, as is the case in most Therapsids including the Deinocephalians such as *Jonkeria* and *Moschops*. This free coracoid is, hower, encountered in a number of Deinocephalians, e.g. *Struthiocephalus, Tapinocephalus, Pelosuchus,* etc.

RADIUS (fig. 2*d*)

The radius is much shorter than the fibula. It is a fairly slender bone somewhat flattened dorso-ventrally; its proximal end is expanded to about twice the width of the distal end, but the shaft has no waist-like constriction.

MANUS (plate XVIII*b* and fig. 4)

When the manus came to my notice it had also been partially prepared, but all the constituent bones were still joined to each other by matrix. I also embedded the whole in a block of plaster before continuing the preparation. As is evident from the photograph, the first digit lies extended, the second and third folded inwards, in the fourth digit the phalanges have been displaced and the fifth lies extended. In the proximal row of the tarsus the intermedium and ulnare have been displaced medially (anteriorly).

In Fig. 4 I give a restoration of the dorsal aspect of the manus. In the proximal row of the carpus there are a radiale, intermedium and ulnare. The radiale is roughly rectangular in outline; dorso-ventrally compressed; it is thickened distally and proximally to form facets for the distals (1 & 2) and radius respectively, with both the dorsal and ventral surfaces concave antero-posteriorly. The intermedium is a fairly small thin flat bone.

The ulnare is the longest bone of the proximal row. It is a stout bone, proximally thick and knob-like, with a large convex proximal facet for the ulna; anteriorly it is weaker, with a flat distal articular facet for the distals (4 and 5); just behind the distal face the bone has a constricted waist.

The centrale is not preserved, but was probably a fair sized bone lying anterior to the intermedium and between the distal ends of the radiale and ulnare, articulating distally with two distals (2 and 3).

There are 5 distal carpals. The first is a small pebble-like bone; the second is the largest of the distals, its dorsal surface is excavated with ridges

on the preaxial, distal and proximal edges; the third also has an excavated dorsal surface; the fourth and fifth are pebble-like.

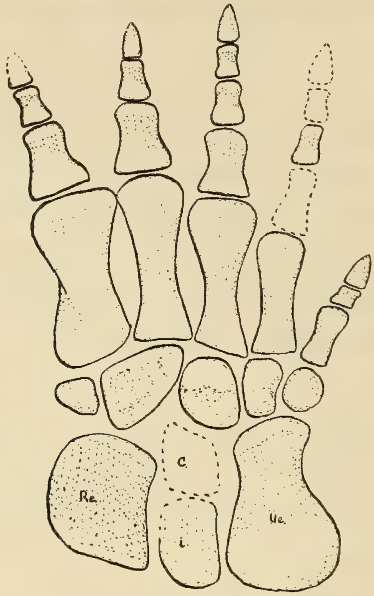


FIG. 4.—*Micranteosaurus parvus* Gen. et Sp. Nov. S.A.M. 4323, Commonage, Merweville, Beaufort West District. Semi-diagrammatic restoration of right manus seen in dorsal view × plus-minus ½. C.—centrale; I—intermedium; Re—radiale; Ue—ulnare.

As a whole the carpus is very Pelycosaur-like, approaching that of *Ophiacodon* fairly closely, except that there is only one centrale.

The metacarpals are somewhat dorso-ventrally flattened bones in general rod-like with slightly constricted waists; the decrease in size from the first to the fourth is fairly evenly graded, but the fifth is much reduced; the first metacarpal is distinguished by being much broader than the others and thus relatively more flattened with expanded ends.

In the first digit the first phalanx is broad proximally, with a waist situated in the anterior half; the distal end is much narrower than the proximal; the second phalanx is much smaller, also broader proximally than distally, with the waist nearly in the middle; anterior to the second roughly hourglass-shaped phalanx there is preserved the proximal end of the ungual phalanx, so that in the first digit there are 3 segments. This is most unusual, but there is no doubt that such is the case. Even without the preserved proximal end of the ungual phalanx the count would also be 3, for the second phalanx with its hourglass-shape could not possibly be an ungual phalanx.

In the second digit there are also 3 segments with each of the constituent phalanges closely resembling those of the first digit.

The third digit has four segments.

The phalanges of the fourth digit have been displaced and all but one lost. What I believe to be the second phalanx lies above the displaced fourth metacarpal. The fourth digit probably had 4 segments as is the case in the third digit.

The fifth digit is much reduced with a short hourglass-shaped first phalanx and a fairly high, narrow and long ungual phalanx.

The carpal formula is thus 3, 1, 5, and the phalangeal formula 3, 3, 4, 4?, 2, and in structure thus near that of the Pelycosaurs.

A Moschopid Carpus (fig. 5)

For comparison I am including here a figure of a carpus, which, on the humerus, I have identified as a Moschopid fairly near *Moschops*. This specimen, S.A.M. 9157, collected by me at Wolwefontein, Prince Albert, consists of a good humerus, radius and ulna, with elements of the carpus still joined by matrix to the distal end of the epipodial in natural articulation.

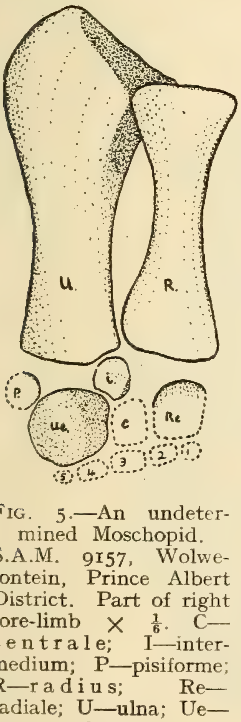


FIG. 5.—An undetermined Moschopid. S.A.M. 9157, Wolwefontein, Prince Albert District. Part of right fore-limb × $\frac{1}{6}$. C—centrale; I—intermedium; P—pisiforme; R—radius; Re—radiale; U—ulna; Ue—ulnare.

In the proximal row there are four bones, viz. radiale, intermedium, ulnare and pisiforme. Only the proximal part of the radiale is preserved, but it would appear that the complete bone was a strong rounded element. The intermedium is nearly circular in outline, with its dorso-ventral diameter about equal to the antero-posterior diameter, and it is thus not a thin plate-like bone. The ulnare is a large bone, subcircular in outline; a longitudinal ridge divides its dorsal surface into two faces, of which the postaxial one is the larger; it is a much thinner bone than the radiale and intermedium, and its under surface is deeply concave.

Postaxially there lies a pebble-like pisiforme.

In between the ulnare and the radiale there was a fair sized centrale; the actual bone has been lost, but an impression in the matrix on the preaxial surface of the ulnare indicates its position. None of the five distals is preserved.

This Moschopid carpus is thus structurally close to that of the Pelycosaurs, but the shape of the individual bones is quite different, whereas in *Micranteosaurus* the individual bones very closely resemble those of the Pelycosaurs in shape.

Taxonomic

Although we know nothing about the posterior two thirds of the skull, the snout is sufficiently characteristic to enable us to establish its affinities. The dorsally curving alveolar border of the premaxilla, the long simple intermeshing incisors, the short postcanine series; the fairly narrow, high snout, and the position of the nostril show that this small Titanosuchid is structurally nearly akin to the large *Anteosaurus*. Because of this great difference in size I propose that it be considered a new genus, under the name *Micranteosaurus parvus* Gen. et Sp. Nov. With *Anteosaurus* it is to be included in the Titanosuchid family Anteosauridae.

Plate XVIII. *Micranteosaurus parvus* Gen. et Sp. Nov. S.A.M. 4323, Commonage, Merweville, Beaufort West District. *a*, Pes. The proximal segment shows the ventral surface of the intermedium and fibulare as these two bones have been turned upside-down in the original preparation. This error is corrected in the restoration (Fig. 3) × about $\frac{2}{3}$ nat. size. *b*, Manus in dorsal view × about $^4/_9$ nat. size.

10. *Paranteosaurus, Gen. Nov.: A Titanosuchian Reptile.* By L. D. Boonstra, D.Sc.

(With 2 text-figures)

In 1940 I collected parts of a skull, a proximal end of a femur and a vertebra of a Titanosuchian on the farm Mynhardtskraal, Beaufort West (S.A.M. 11485). The cranial material consists of a weathered pre-orbital part and the dorsal cranial roof without actual contact. The snout on development yielded a good palatal exposure (Fig. 1), and in the other part the interorbital region and the structure of the postorbital bars could be determined (Fig. 2).

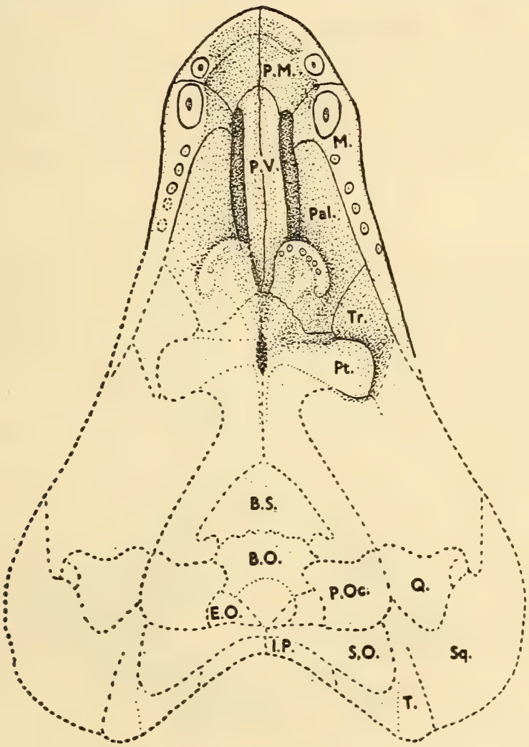


Fig. 1.—*Paranteosaurus primus* Gen et Sp. Nov. Orthoprojection of the Ventral View of the skull of the holotype, S.A.M. 11485, Mynhardtskraal, Beaufort West. (× $\frac{1}{6}$.)

The palate as shown in Fig. 1 agrees very closely in structure to that of the Titanosuchian genus *Anteosaurus*. As in *Anteosaurus* the alveolar border of the premaxilla does not lie in the same plane as the maxillary border, but curving upwards makes an obtuse angle just anterior to the canine; on both sides only the root of the last incisor is preserved, with anteriorly a matrix-filled groove with little indication of a division into separate alveoli; in the left maxilla there is in this groove room for two incisors and in the right possibly for three; the incisor count thus falls within the limits set for *Anteosaurus;* the canines have only the roots preserved, but these indicate that the canines were directed much more anteriorly than in *Anteosaurus;* as is usual in *Anteosaurus*, five irregularly spaced small postcanines are present; these are small labio-lingually flattened conical teeth; in a horizontal fracture through the right maxilla a replacing root is seen lying linguo-anteriorly to the third postcanine. The crescentic dentigerous boss on the palatine and the relations of the premaxilla, prevomer, maxilla, palatine, transversum and the pterygoid are as in *Anteosaurus*.

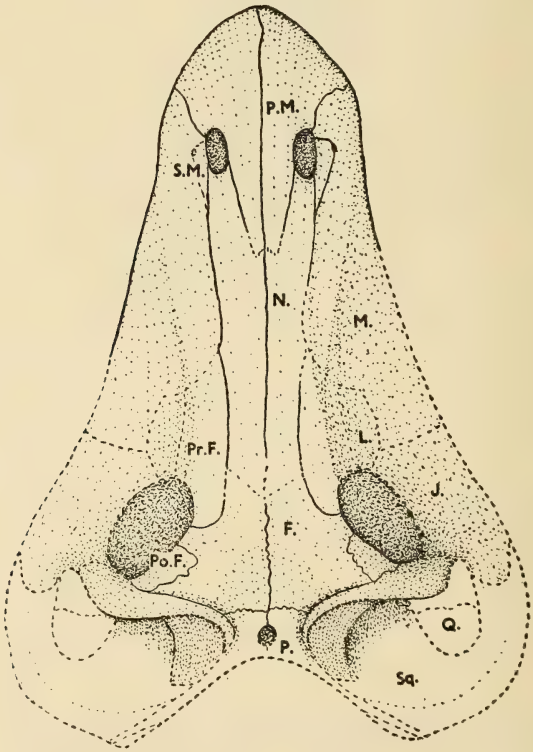


FIG. 2.—*Paranteosaurus primus* Gen. et Sp. Nov. Orthoprojection of the dorsal view of the skull of the holotype, S.A.M. 11485, Mynhardtskraal, Beaufort West. (× $\frac{1}{8}$.)

On the basis of the palate alone there is nothing to exclude the specimen from the genus *Anteosaurus*. Similarly the outer surface of the snout (Fig. 2) is very similar to that of *Anteosaurus*, although the snout is relatively lower.

But in the structure of the skull roof and particularly of the postorbital bar our specimen differs very markedly from *Anteosaurus*. This marked difference is due to the small size of the postfrontal, which is here a small bone forming the dorso-posterior orbital margin, whereas in *Anteosaurus* the strong pachyostotic development of the postfrontal has resulted in this element overflowing on to the surface of the frontal and overgrowing much of the postorbital and forming the prominent boss so characteristic of *Anteosaurus*. An intermediary stage between the condition of the postfrontal in this specimen and in *Anteosaurus* is shown by the Russian genus *Titanophoneus*. The postfrontal in *Pseudanteosaurus* with its posterior tongue-like prolongation is of quite a different nature.

No features in this skull, which may be thought to indicate youthfulness, are not also encountered in some species of *Anteosaurus*. I thus conclude that the smallness of the postfrontal and the light build of the postorbital bar do not represent a growth-stage in the individual, but are in fact a retention of an older morphological stage of the family Anteosauridae.

Taxonomic

For this new form of the Anteosauridae I propose the name *Paranteosaurus primus* Gen. et Sp. Nov. It may be characterised as follows:

A medium-sized Anteosaurid (max. length probably about 570 mm.), with small postfrontal not extending posteriorly, lightly built postorbital bar, without any sign of a boss-like development in the upper part of the postorbital bar, dental formula i.3?-4?, c.1, p.c.5.

REFERENCES

Boonstra, L. D. 1954. The Cranial Structure of the Titanosuchian: *Anteosaurus*. Ann. S. Afr. Mus. 42, 2, 106-148.

Efremov, J. A. 1940. Preliminary Description of the New Permian and Triassic Tetrapoda from U.S.S.R. Acad. Sc. U.S.S.R., 10, 2, 1-140.

ANNALS

OF THE

SOUTH AFRICAN MUSEUM

VOLUME XLII

Descriptions of the Palaeontological Material acquired by the South African Museum and the Geological Survey of South Africa.

PART III, *containing:*—

ISSUED JANUARY 1955. *PRICE £1 10s. 0d.*

PRINTED FOR THE

TRUSTEES OF THE SOUTH AFRICAN MUSEUM

AND THE

GEOLOGICAL SURVEY OF SOUTH AFRICA

BY THE NATIONAL COMMERCIAL PRINTERS LIMITED,

JAN VAN RIEBEECK STREET, ELSIES RIVER

11. *Some Fossil Mammals in the South African Museum Collections.** By

H. B. S. Cooke, D.Sc., F.R.S.S.Afr. Johannesburg.

(With map and Plate XIX.)

Abstract

The collections of the South African Museum at Cape Town include the first fossil mammal to be discovered in Southern Africa, *Homoioceras bainii*. There are also some two hundred fossil teeth and bones of Quaternary mammals from twenty-four sites, eleven of which have not previously been recorded. Few of the specimens have been mentioned in published literature unless they represented new species, and lists of faunal assemblages exist only for two of the sites — Taung and Florisbad. The present account records all the species identified in the collections and lists the assemblages for each locality.

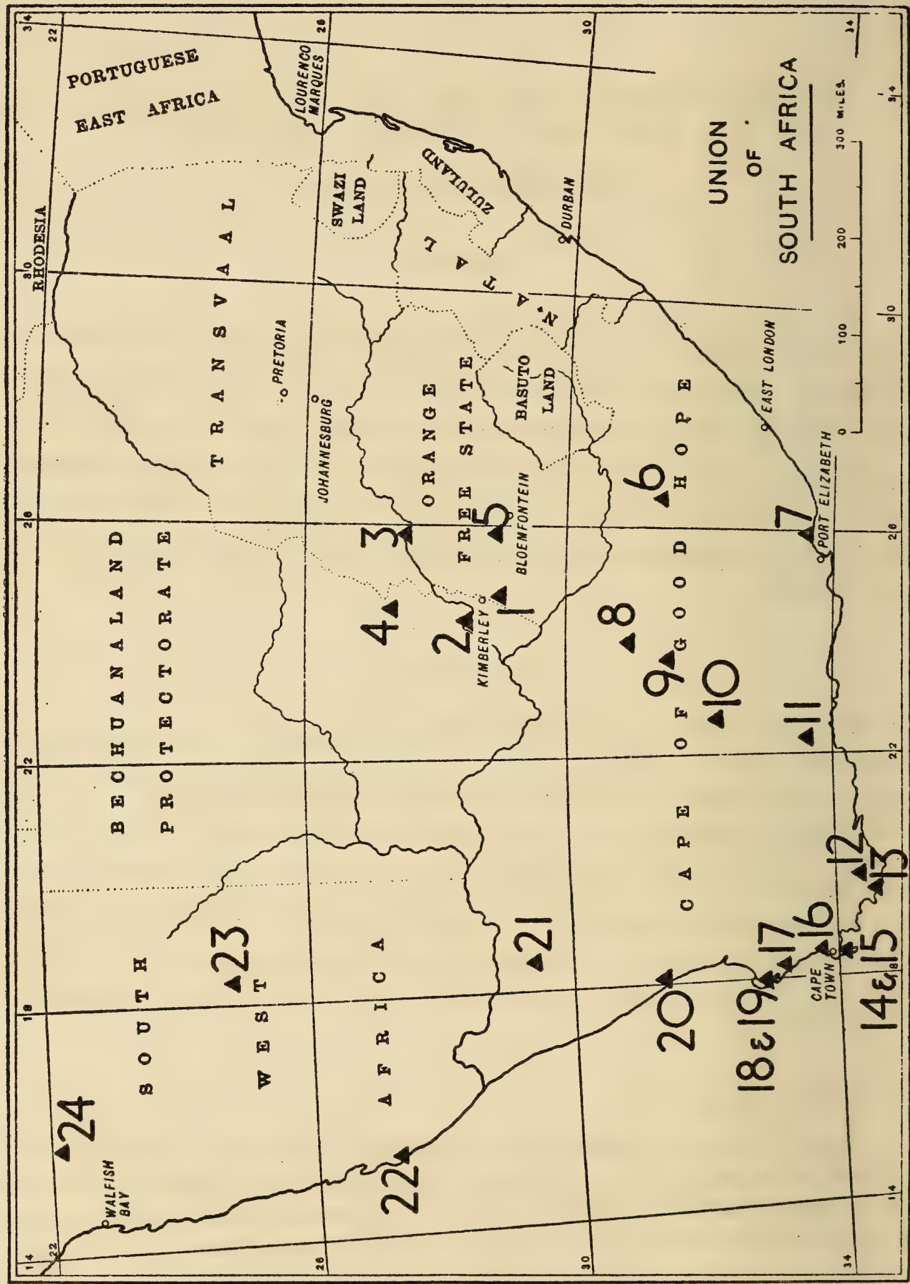
Introduction

The fossil collections of the South African Museum at Cape Town include some two hundred bones and teeth of Quaternary mammals of which only very few specimens have been mentioned in published literature. Twenty-four sites are represented, eleven of these being new records. Of the thirteen known localities, faunal assemblages have been listed only for two — Taung and Florisbad — while the remaining eleven sites have been recorded merely by the mention or description of isolated specimens. It is the purpose of this account to provide as complete a record as possible for the assemblages for each locality. The accompanying map shows the wide distribution of the sites.

1. *Modder River, O.F.S.*

One of the most striking of the Quaternary mammalian specimens displayed in the South African Museum is the frontlet and gigantic horn cores of an extinct buffalo, *"Bubalus" bainii*. The remains were recovered from a depth of forty feet in alluvial deposits of the Modder River, in the Orange

* Read before Section D of the South African Association for the Advancement of Science at its Jubilee Congress in Cape Town, July, 1952.


PORTUGUESE EAST AFRICA
RHODESIA
LOURENCO MARQUES
SWAZI LAND
ZULULAND
DURBAN
NATAL
TRANSVAAL
PRETORIA
JOHANNESBURG
ORANGE FREE STATE
BASUTO LAND
BLOEMFONTEIN
KIMBERLEY
BECHUANALAND PROTECTORATE
SOUTH WEST AFRICA
WALFISH BAY
CAPE OF GOOD HOPE
EAST LONDON
PORT ELIZABETH
CAPE TOWN
UNION OF SOUTH AFRICA
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Free State in 1839. The remarkable civil engineer and naturalist, Andrew Geddes Bain, saw the specimen and persuaded the actual finder, Mr. Martin Smith, to send it to the Geological Society of London. Its subsequent history is uncertain but it was displayed in the South African Museum and was seen by the eminent English palaeontologist, Dr. Seeley, who described it in 1891 under the name *Bubalus bainii.**

Several other specimens of this giant buffalo have since been found in South Africa and three related species have been described from North Africa (1951), East Africa (1933) and the Anglo-Egyptian Sudan (1949). In describing the Sudan specimen, the late Miss D. M. A. Bate (1949, 1951) created a new genus *Homoioceras* for the African long-horned buffaloes and showed that this genus is allied to the African *Syncerus* and is very distinct from the Asiatic *Bubalus*. The South African form is accordingly now *Homoioceras bainii* (Seeley).

Another fossil is recorded as coming from the banks of the Modder River "half way between Kimberley and Bloemfontein". It comprises an imperfect frontlet and partial horn core of a large hartebeest, described by Broom in 1909 and named *Bubalis* [*sic*] *priscus*. If Broom's generic reference is correct it should now be placed in *Alcelaphus* as *A. priscus,* but it is possible that it might fall within the genus *Peloroceras*.

2. *Delport's Hope, Vaal River*

The fauna from this site has been listed by the writer (1949) from material in the McGregor Memorial Museum, Kimberley. The South African Museum collection includes a number of bone fragments from which only the proximal end of a right metacarpal can be identified as belonging to a large bovid, possibly a kudu.

3. *Sheppard Island, Vaal River*

When material from this site was listed by the writer in 1949, it was thought that some of the specimens collected by van Riet Lowe in 1928 had been destroyed in a fire at the University of the Witwatersrand in 1931. Six of these have now been found in the S.A. Museum collections. The species represented are *Equus sandwithi, E. capensis, E. burchelli, Syncerus caffer,* and possibly, a kudu.

4. *Taung*†

In 1920 Haughton described seven small skulls of baboons from the limestone deposit at Taung but the full paper was not published. The name

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* See Appendix, p. 168.

† Union of S. Afr. Rep. Form and Spelling of Geographical Proper Names, 1939, recommended "Taung"' instead of the previous "Taungs".

Papio antiquus was proposed and was printed in an abstract (1924). In 1926 J. H. S. Gear collected additional material and distinguished two species, the larger of which he named *Papio africanus* and the smaller *P. izodi,* presumably regarding Haughton's name as a nomen nudum. In 1940 the generic reference was transferred by Broom to *Parapapio* and Gear's views were upheld. In 1948, however, Broom re-examined Haughton's original specimens (which are in the S.A. Museum) and concluded that only the larger species was represented and that the original specific name *antiquus* must be held to ante-date *africanus*. The neotype skull of the species is numbered S.A.M. 5356 and the best jaw is S.A.M. 5357. The generic reference remains amended and the correct designation is now *Parapapio antiquus* (Haughton).

5. *Florisbad (Hagenstad Salt Pan)*

The S.A. Museum collections include a selection of specimens from the spring deposit at Florisbad first described briefly by Broom (1913) and later by Dreyer and Lyle (1931), whose list is complete but subject to several specific amendments. The assemblage includes the following species: *Pedetes hagenstadi, Aonyx robustus, Diceros bicornis, Equus quagga, E. lylei, E. capensis, Hippopotamus amphibius, Phacochoerus helmei, P. compactus, P. aethiopicus, Homoioceras bainii, Pelea capreolus, Pelorocerus helmei, Connochaetes antiquus* (?), *Damaliscus albifrons, Taurotragus oryx, Strepsiceros strepsiceros, Gazella bondi* (?), *Antidorcas marsupialis, Cephalophus* sp., *Sylvicapra grimmia*.

6. *Hoogstede, Tarkastad District*

Five specimens from the farm Hoogstede, west of Queenstown, are lightly mineralised and are probably surface finds. One specimen is a tooth of a domestic ox. The remainder represent a lion, *Equus burchelli* and *Pelorocerus* sp., possibly *P. broomi*.

7. *Zwartkops, Sundays River*

A small fragment of an upper molar of *Hippopotamus* sp. is the only fossil mammal from this locality, which has yielded much invertebrate material to other collections.

8. *Victoria West*

From the farm Jakkalsfontein near Victoria West comes an upper molar of *Equus burchelli*. There is an upper premolar of *Equus capensis* from an unknown locality in the same area.

9. *Brakfontein, Three Sisters*

A single specimen from the farm Brakfontein, near Three Sisters, is a fragment of a left lower jaw of *Diceros bicornis*.

10. *Beaufort West*

A lightly mineralised milk molar of *Equus* cf. *burchelli* comes from the farm Little England near Beaufort West.

11. *Cango Caves, Oudtshoorn*

Six specimens from the Cango Caves are referable to *Procavia capensis, Connochaetes* sp. and *Tragelaphus* cf. *scriptus*.

12. *Linkerhandsgat and Nooitgedacht, Stanford*

A few miles north-east of Stanford is an unusual occurrence of chalky limestone and calcified sands containing bones and teeth of mammals. Three specimens from Linkerhandsgat are identified as *Crocuta* sp., *Thos mesomelas* and *Alcelaphus* cf. *caama*. From the adjoining farm Nooitgedacht, there are three fragments representing *Redunca arundium* and *Aepyceros melampus*. A larger private collection and material collected by the writer will be dealt with at some length in a separate paper.

13. *Hawston*

The sand-dunes along the coast near Stanford and Hawston have yielded almost unmineralised teeth of the African elephant and of the black rhinoceros.

14. *Skildegat Cave, Fish Hoek*

This cave, also known as Peers' Cave, was excavated twenty-five years ago by B. and V. Peers and it is probable that the eight teeth from this locality which are in the S.A. Museum collections were recovered during the excavations. A bovid incisor cannot be determined generically but the remaining specimens belong to *Equus zebra* and *E. capensis*.

15. *Kalk Bay*

This area yielded three molars of *Hippopotamus amphibius* and part of a lower molar of *Loxodonta africana*.

16. *Yzerplaats, Maitland District*

The type series of teeth of *Equus capensis*, described by Broom in 1909 and figured in 1928, was contained in a block of limestone washed up on the beach at Yzerplaats.

17. *Bloembosch, Darling District*

The dune-covered farm Bloembosch, north of Yzerplaats, has furnished nearly fifty specimens, including bones, imperfect jaws and isolated teeth. *Equus capensis* is abundant, the collection including the plesiotype upper left second molar referred to Broom's species by Haughton (1932). Other equine material is not specifically identifiable except for an unmineralised lower jaw of a young *Equus zebra*. *Diceros bicornis* occurs. The only carnivore is *Crocuta crocuta*. Artiodactyls include *Hippopotamus* cf. *amphibius, Giraffa camelopardalis, Homoioceras bainii, Syncerus caffer, Connochaetes* sp., *Hippotragus* cf. *niger*. The two lower mandibles which the writer (Cooke 1947) named *Hippotragus problematicus*, are also in the collection; it was suggested that these jaws might represent the almost unknown *H. leucophaeus* but Dr. Broom informed the writer shortly before his death that he had found material of the Blue Buck during his last European-American tour and that the Bloembosch fossil was clearly distinct. His notes and drawings have not so far been found.

The recently discovered site at Elandsfontein, near Hopefield, which is being studied by the University of Cape Town, has yielded abundant fossil material of a character similar to the Bloembosch specimens;* it has also provided a fossil human cranium.

18. *Saldanha Bay*

The only species represented by the five isolated teeth from this locality is *Equus capensis*. One of the specimens is the isolated upper fourth premolar described by Broom (1913) as "from Darling", and another is the plesiotype left lower premolar described by Haughton (1932).

19. *Hoedjiesbaai*

The limestone quarries at Hoedjiesbaai, near Saldanha Bay, have furnished sixteen very nice specimens, mostly partial jaws with teeth. The five species are *Procavia* cf. *capensis, Thos mesomelas, Arctocephalus pusillus, Suricata* sp. (or possibly *Cynictis*), and *Raphicerus campestris*. This is believed to be the first record of the Cape sea lion in the fossil state.

20. *Geelwal Karoo, Van Rhynsdorp District*

This site has provided a partial lower jaw of *Thos mesomelas*.

21. *Near Springbok, Namaqualand*

A site 40 miles east of Springbok yielded the type series of cheek teeth described by Haughton (1932) as *Notohipparion namaquense*. The original illustration exaggerates the breadth of the crowns as the plane of drawing is parallel to the rather oblique grinding surface.

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* See: Following article by R. Singer and E. N. Keen.

22. *Bogenfels, S.W.A.*

The collections include an incomplete lower jaw from Bogenfels, S.W.A., labelled "*Propalaeonyx africanus* Stromer". It comes, presumably, from the so-called Miocene beds.

23. *Kalk Plateau, S.W.A.*

Two equine teeth, apparently of *Equus burchelli*, are recorded as coming from a well on the Kalk Plateau east of Marienthal in S.W.A.

24. *Usakos, S.W.A.*

The type series of upper and lower cheek teeth of *Equus sandwithi* (Haughton 1932), was associated with a number of other specimens not previously mentioned. It is now possible to reconstruct all the cheek teeth, though not of a single individual. One tooth of *Equus capensis* is also represented in the assemblage, and the bovid genera *Connochaetes* and *Strepsiceros* are present but the species cannot be determined.

25. *Other Localities*

The collection includes a lime-encrusted upper premolar of *Equus* cf. *zebra* from Broken Hill, Northern Rhodesia. There is a piece of grey limestone from the vicinity of Mt. Lemagrut (near the famous Olduvai gorge), with part of the left lower jaw of a rhinoceros exposed.

26. *Unknown Localities*

Twenty specimens are without locality records. The species represented are *Equus burchelli, E. kuhni, E. capensis, Hippopotamus* sp., *Damaliscus* sp., *Connochaetes* sp. and *Phacochoerus* sp.

REFERENCES

BATE, D. M. A. 1949. A new African fossil long-horned buffalo. *Ann. Mag. Nat. Hist.* (12), II, pp. 396-398.

BATE, D. M. A. 1951. The mammals from Singa and Abu Hugar. In *Fossil Mammals of Africa*, II, pp. 1-28. British Museum (Nat. Hist.), London.

BROOM, R. 1909. On a large extinct species of Bubalis. *Ann. S. Afr. Mus.* VII, pp. 279, 280.

BROOM, R. 1909. On the evidence of a large horse recently extinct in South Africa. *Ibid.* pp. 281, 282.

BROOM, R. 1913. Man contemporaneous with extinct animals. *Ann. S. Afr. Mus.* XII, pp. 13-16.

BROOM, R. 1928. On some new mammals from the Diamond gravels of the Kimberley District. *Ann. S. Afr. Mus.* XXII, pp. 439-444.

BROOM, R. 1940. The South African Pleistocene Cercopithecid Apes. *Ann. Transv. Mus.* XX, pp. 89-100.

BROOM, R. 1948. Some South African Pliocene and Pleistocene Mammals. *Ann. Transv. Mus.* XXI, pp. 1-38.

Broom, R. and Schepers, G. W. H. 1946. The South African Fossil Ape-men; the Australopithecinae. *Transv. Mus. Mem.* No. 2, pp. 1-272.
Cooke, H. B. S. 1947. Some fossil hippotragine antelopes from South Africa. *S. Afr. J. Sci.* XLIII, pp. 226-231.
Cooke, H. B. S. 1949. Fossil mammals of the Vaal River basin. *Geol. Surv. Mem.* XXXV (3), pp. 1-109.
Dreyer, T. F. and Lyle, A. 1931. New fossil mammals and man from South Africa. *Grey Univ. College Dept. Zool.*, Bloemfontein, pp. 1-60.
Gear, J. H. S. 1926. A preliminary account of the baboon remains from Taungs. *S. Afr. J. Sci.* XXIII, pp. 731-747.
Haughton, S. H. 1924. *Papio antiquus* n.sp. *Trans. Roy. Soc. S. Afr.* XII. Min. & Proc. 19 May, 1920, p. LXVIII.
Haughton, S. H. 1932. The fossil Equidae of South Africa. *Ann. S. Afr. Mus.* XXVIII, pp. 407-427.
Seeley, H. G. 1891. On *Bubalus bainii* (Seeley). *Geol. Mag.* VIII, pp. 199-202.

APPENDIX

Bubalus bainii

The date when the specimen was received at the Museum is not recorded. Two entries in the Account Book for 1856 may refer to this specimen: "March. To Ford repairing horns, £1 15s." Ford had already repaired the models of natives, presumably made of plaster, thus having a knowledge of plaster-work, which would be suitable for the repair of fossils. "September. To G. West, paint for fossil head, 3s. 6d."

The skull was on exhibition over the entrance to the old Museum (now the west wing of the South African Library) in 1860, when Layard compiled his Catalogue: "Immediately overhead is a magnificent fossil frontlet of an extinct bovine from Thaba 'Nchu." (Layard, E. L. *Catalogue of the South African Museum,* Part 1, Mammals, p. 7. Cape Town, 1862. Preface dated 1st January, 1861, publication delayed until 1862. See Annual Report S.A. Mus. for 1862.) It was in the same position when Seeley saw it.

The locality Thaba 'Nchu is not mentioned in Bain's references to this fossil Bovine. Bain did not visit the eastern part of the Orange Free State until 1845. Thaba 'Nchu, however, does lie within the catchment area of the sources of the Modder River. Layard's entry seems to be the only record of the locality, unless possibly a more precise site can be traced by research in the Deeds Office for Mr. Martin Smith's farm — if he possessed one.

In Dr. Cooke's map the site of the locality (No. 1) is placed south of Kimberley in the western part of the Orange Free State; but if Layard was correct it should be placed in the eastern part between Bloemfontein and the border of Basutoland.

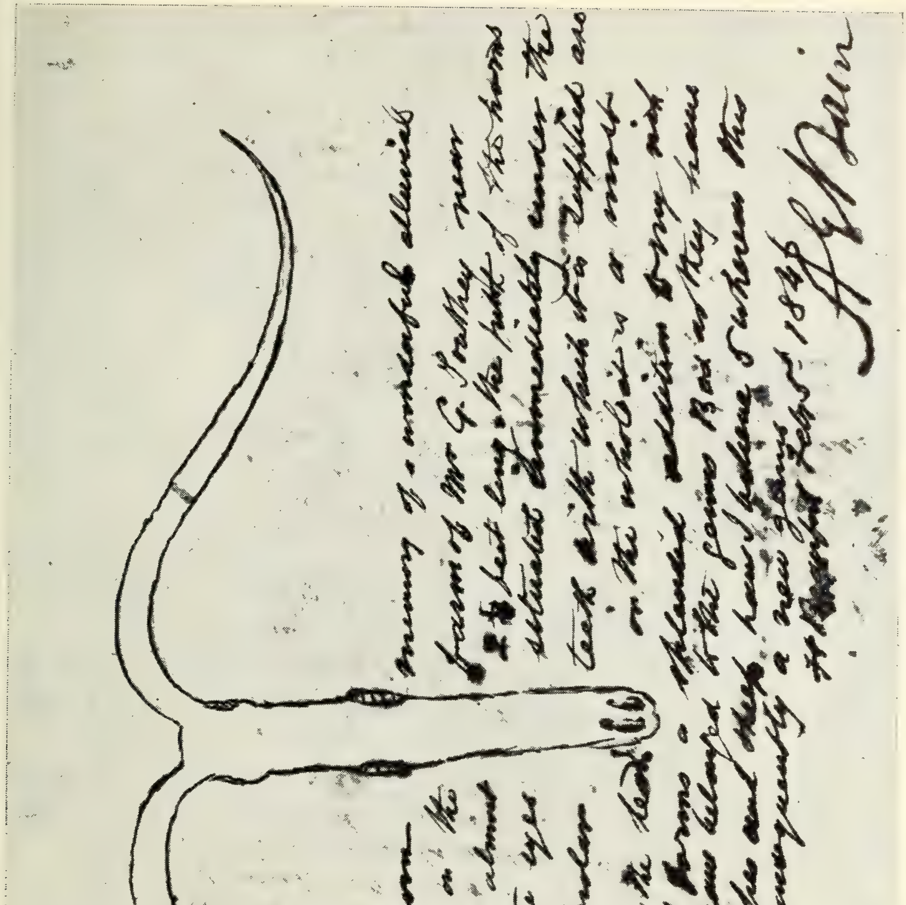
Seeley (p. 201) gave two reasons for considering this type specimen as the one referred to by Bain in 1839. The second reason seems to be acceptable. In his letter to Sir H. de la Beche in 1844, read to the Geological Society in 1845, and printed (abridged) in Trans. Geol. Soc. Lond. (2), VII, 4, 1856, Bain said that Martin Smith's fossil was "in Cape Town". The South African Museum possesses Bain's own copy of this part of the Transactions, in which two words have been added by Bain (p. 59) to make the sentence read: "This fossil is now in *the* Cape Town *Museum.*"

Seeley's first reason is less acceptable because there may be two interpretations. Thomas Bain's words "his father's fossil" may mean either the fossil which his father induced Martin Smith to send to Cape Town, or an example which A. G. Bain himself found.

It is, therefore, appropriate to reproduce here (pl. XIX) Bain's MS. drawing and description (from memory) of a specimen of this bovine which he himself found on Mr. G. Southey's farm near Graaff-Reinet. The original sketch is in the S. Afr. Museum library — but what happened to the specimen?

See: Lister, M. H. *Journals of Andrew Geddes Bain.* Van Riebeeck Soc. Publ. No. 30, p. 230. Cape Town, 1949. Also Seeley, H. G., 1891 (*op. cit. supra*).

[Ed.]



The above is an outline, from memory of a wonderful alluvial
fossil which I discovered on the farm of Mr G. Southey near
Graaff Reinet. The head is almost 2½ feet long. the pith of the horns
12½ feet, the orbit of the eyes situated immediately under the
horns and the <u>four</u> molar teeth with which it is supplied are
more than half way up the head. On the whole it is a most
singular animal and forms a splendid addition to my col-
lection. It could not have belonged to the genus Bos as they have
molars, the antelopes and sheep have I believe 5 whereas this
only four and is consequently a new genus

Ft Beaufort Feb 5th 1846

A G Bain

12. *Fossil Suiformes from Hopefield.** By R. Singer and E. N. Keen.

Anatomy Department, University of Cape Town.

(With Plates XX—XXIV and 1 text-figure.)

Introduction

The fossil site on the farm "Elandsfontein" situated 10 miles south-west of Hopefield, 90 miles north of Cape Town, was located by one of us (R.S.) in May, 1951.† On numerous subsequent visits various members of the University of Cape Town staff, Professor M. R. Drennan, Messrs. J. A. Mabbutt, K. Jolly and the authors, have collected highly fossilized bones and stone implements from the surface of the site. The range of specimens already identified includes a large number of extinct and existing mammals, the proportions of which suggest an early Upper Pleistocene period, with the possibility of extension into the late Middle Pleistocene.

In January, 1953, Jolly, on a field trip with Singer, discovered pieces of the greater portion of the calvarium of an hominid. On three subsequent expeditions Jolly and Singer retrieved additional portions of the cranium which has since been reconstructed (Drennan, 1953; Singer, 1954). Fluorine tests, carried out through the courtesy of Dr. K. P. Oakley of the British Museum, reveal that this Saldanha Skull and the *Mesochoerus* fossils (described in this paper) were apparently contemporaneous.

Elandsfontein lies in the sandy veld between the Sout River and the Langebaan-Saldanha Lagoon. The site is 300 feet above sea-level and is divided into wind-scoured kloofs or depressions by sand-dunes which are either drifting or, where covered by vegetation, stationary. Ridges of ferricrete cut diagonally across the length of the site, and in places the dunes are capped by massive calcrete mounds or flat boulders of partly silicified surface limestone. Softer, cellular calcretes are found in certain places at

* Simpson (1945) has given reasons for placing the *Hippopotamidae* and the *Suidae* into the separate infraorders ANCODONTA and SUINA; both are, however, included in the suborder SUIFORMES.

† The existence of fossil-bearing sites in the Darling-Hopefield district has been known for years (Broom, R., Annals S. Afr. Mus. VII, p. 281, 1909, and XII, p. 13, 1913; Cooke, H. B. S., XLII, p. 161, 1955), but hitherto no thorough investigation of the area had been made.

the lowest parts of the depressions. The tortuous courses of the ferricrete ridges indicate that they are the indurated lower flanks of old sand-dunes now stripped bare of the sand walls. This ferruginization is usually associated with moist ground conditions, a fairly high stable water-table and an abundance of vegetable acids in the soil. It seems that this fossil site was at one time a large vlei or lagoon along the edge of which animals roamed.

The rich collections of stone implements indicate the presence of Man on the site from a late stage of the Chelles-Acheul (Stellenbosch) Culture until the period when the Bush races were developing their culture. The occupation is not a continuous one. A large number of the implements exemplify the transition from the South African Earlier to the Middle Stone Age.

DESCRIPTION OF MATERIAL

Fam. HIPPOPOTAMIDAE

Hippopotamus amphibius Linnaeus 1758

The collection of fossil mammalian remains from the Hopefield site includes several fragments of jaws and teeth which are identified as hippopotamus remains. Many of the specimens derive from young animals and show deciduous or unerupted permanent teeth. Six of the permanent molar teeth are complete and can be compared in size with the limits stated in Cooke's (1949) survey of all the South African fossil material recovered up to that date. None of the measurements fall outside the wide limits which are characteristic of this species. There are therefore no grounds for separating the remains from the existing species *Hippopotamus amphibius*, fossil specimens of which have been found in several other South African localities.

Fam. SUIDAE

Genus *Mesochoerus*, Shaw and Cooke, 1941
Mesochoerus lategani, sp. nov.

Diagnosis: A *Mesochoerus* resembling *M. olduvaiensis* (Leakey, 1942) in the structure of the third lower molars. The second lower molars have a well developed anterior median pillar. The crowns of the third lower molars are longer by 10% and narrower by 10%, and the height of the unworn pillars is greater by 10% than in *M. olduvaiensis*. The pillars of the upper molars are obliquely arranged, those on the labial side being placed slightly in front of their lingual partners. The fourth premolars are molariform.

Type: The complete upper and lower cheek dentition of a single animal, recovered in seven fragments numbered S6, S7, S8, S14, S15, S16, S17 in the Hopefield collection in the Anatomy Dept., University of Cape Town. (Plate XX.) Specimens S7, S14, S16 and S17, constituting the right dentition.

have been donated to the S.A. Museum where they have received catalogue number 11712.

Among the fossil specimens collected from the Hopefield site are several upper and lower teeth and partial jaws which appear to belong to a single species of large suid. All the fossils at Hopefield have been more or less damaged by the movement of the sand in which they lie. For this reason recovery of an intact jaw is uncommon, and the study is necessarily confined to the characters of the individual teeth, which are often found lying free and not close to any other teeth or suid remains.

The collection consists of teeth and jaws from ten individuals and includes a complete upper and lower molar dentition of a single animal (S6: left M_3 M_2 M_1; S15 and S8: left M^3 M^2 M^1; S16 and S17: right M_3 M_2 M_1 P_4 P_3; S14 and S7: right M^3 M^2 M^1 P^4). Three other pairs of left and right lower third molars (S2 and S3, S12 and S13, S9 and S9a) appeared to derive from a single animal in each case, and one pair of right and left upper third molars (S11 and S10) similarly resembled each other. These upper molars could not, however, be made to occlude satisfactorily with any of the lowers. Five individuals are represented by isolated teeth (S1, right M_3; S4, right M^3; S5, left M^3 and M^2; S20, left M^3 and M^2; and S21, right M_3).

The various teeth resemble each other sufficiently closely to support the conclusion that only one species is represented.

Lower Cheek Teeth

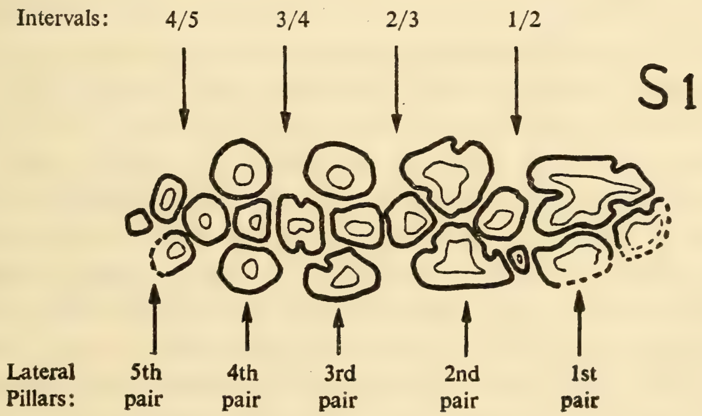


Fig. 1.

Third lower molars: ten specimens from six individuals. A typical specimen in moderate wear is illustrated in Fig. 1, which also shows the convention by which the lateral and median pillars are identified. The crowns of these

teeth are each made up of five pairs of lateral pillars arranged symmetrically (S1, S2, S6, Pl. XXI). Each pair appears to meet in the median line of the tooth early in wear, but becomes separated by median pillars in later wear. The usual number of median pillars is nine. A single median pillar is found in front of the first lateral pair, sometimes in the median line, sometimes leaning to the labial side of the tooth. There are two median pillars in the 1/2, 2/3 and 3/4 intervals. These may be of equal size, or the posterior one may be larger than the anterior. A single median pillar is usual in the 4/5 interval, and another in the posterior median position, i.e. at the posterior extremity of the tooth. A few of the specimens show duplication of the median pillars in the 4/5 and posterior positions.

The tooth erupts in such a way that the first three pairs of lateral pillars rapidly come into wear one after another, beginning in front (Pl. XX, B). Wear commences in these anterior pillars before the fourth and fifth pairs erupt. Later on growth and subsequent wear proceed at a faster rate in the posterior part of the tooth, so that in late wear the tooth may present an appearance of relatively even attrition. The upper third molars erupt in a similar way.

In general the pattern of the worn surface of the lower tooth is simpler, less complex and less folded than that of the corresponding upper tooth.

There is a cingulum at the crown-root junction in all specimens, but in some it is very poorly developed (S21, Pl. XXII). In many of the teeth the crown is partially covered with a thick layer of cement (S21, Pl. XXII).

Roots are very well developed along the whole length of the tooth, even at the stage when the posterior pillars are neither fully developed nor erupted (S21, Pl. XXII); at this stage the length of the root may exceed the height of the crown. The roots supporting the anterior three pairs of lateral pillars are more or less separated from their neighbours, and straddle a wide dental canal (S16, Pl. XXII, D). In some cases the tips of these roots are distorted in quite irregular ways (S9, Pl. XXIII, B). Extra median rootlets are occasionally present in both upper and lower third molars, and vary from a minute nodule to a spicule as long as the neighbouring lateral roots (S4, S14, Pl. XXIV). The curvature of the roots is backwards and to the labial side; the labial roots are always larger than those on the lingual side of the tooth. The roots of the posterior two pairs of lateral pillars tend to be fused together to form flat plates arranged antero-posteriorly. Towards the back of the tooth these plates converge, and fuse together in the median line of the tooth, under the posterior median pillar (cf. Pl. XXIV, D, S4).

	Dimensions of Crown in mm. Greatest Length.	Greatest Breadth.	Occlusal Breadth.	Height of unworn pillars above root. 2nd pillar.	3rd pillar.	4th pillar.	5th pillar.	Proportions of Crown. Length/Breadth.	Height/Breadth.	Length/Height.	Length of roots in mm. Anterior.	Posterior.
S1 (R)	73	22	20	—	—	—	21	3·3	—	—	—	20+
S2 (L)	—	22	20	—	—	—	—	—	—	—	—	—
S3 (R)	67	22	20	—	—	—	—	3.0	—	—	—	40
S6 (L)	75	23	16	—	—	—	—	3·3	—	—	33	12
S16 (R)	77	22	15	—	33	—	—	3.5	1.5	2.3	32+	10
S9 (L)	—	24	22	—	—	—	—	—	—	—	—	26
S9a (R)	—	23	21	—	—	—	—	—	—	—	—	30
S12 (L)	75	21	16	—	28	28	25	3.6	1.3	2.7	30	—
S13 (R)	75	21	16	—	27	—	—	3.6	1.3	2.8	28	—
S21 (R)	—	21	—	26	29	28	—	—	1.4	—	—	16+
Mean	73·7	22.1	18.4		29.2			3·4	1.4	2.6		
Mesochoerus olduvaiensis												
Holotype	67.5	25	17	—	—	26	—	2.7	1.0	2.6	—	—
Paratype	65	24	17	—	—	26	—	2.7	1.1	2.5	—	—
Mesochoerus paiceae												
Holotype	70	23	22	—	—	—		3.0	—	—	—	—
Neotype	68	22	—	34	34	32		3.1	1.5	2.0	14	—

Table I: Dimensions of Third Lower Molars, and comparison with the reported dimensions of *Mesochoerus olduvaiensis* and *Mesochoerus paiceae*.

Figures are omitted where the specimen is broken, insufficiently worn, or insufficiently developed.

Second lower molars: three specimens from two individuals. The crowns of these teeth are made up of two symmetrically placed pairs of lateral pillars, a single well developed anterior median pillar, two median pillars in the interval between the lateral pairs, and a fairly large posterior median pillar. The anterior median pillar is eccentrically placed on the labial side of the tooth, and the posterior median pillar on the lingual side of the median line (S6, Pl. XXI, B). In the two specimens in which the pattern is clear there are small accessory enamel nodules behind each labial lateral pillar and a small row of nodules at the extreme anterior part of the tooth, in front of the anterior median pillar (S17, Pl. XXII, E).

There are four well developed separate roots, which appear to diverge whether the tooth is viewed end-on or from the side. The general curvature of the root is backwards and to the labial side (S17, Pl. XXII, F). The posterior roots are larger than the anterior.

	Dimensions of Crown.			
	Greatest Length.	Greatest Breadth.	Occlusal Breadth.	Length of Roots.
S3 (R)	24	20	—	—
S6 (L)	29	18	16	—
S17 (R)	30	20	14	29
Mean	28	19	15	
Mesochoerus olduvaiensis				
Holotype	28	20	17	—
Paratype	29	21	18	—
Mesochoerus paiceae				
Neotype	32	19	18	20-25

Table II: Dimensions of Second Lower Molars in mm., and comparison with the dimensions reported for *M. olduvaiensis* and *M. paiceae*.

First lower molars: two specimens from different individuals. Both these teeth are extremely worn (S6, Pl. XXI, B; S17, Pl. XXII, E). The second and third molars belonging to each of these first molars have been found, and it can be seen that at the time when the first molar was worn down to the roots, the posterior part of the third molar was incompletely developed and unerupted (S6, Pl. XXI, B). The degree of wear of these teeth precludes a determination of the enamel pattern in the earlier stages of wear. In each there remain two fairly large convoluted pillars, one in front of the other, with small islands of enamel in the centre of the outlines, indicating an originally more complex pattern from which the present appearances were derived.

There are four roots, as in the second molar, diverging in both views, the posterior roots being more massive than the anterior (S17, Pl. XXII, F; S6, Pl. XX).

The greatest length, greatest breadth, and occlusal breadth of the crowns of the two teeth are 20, 14 and 12 mm. (S17); 20, 14 and 14 mm. (S6), respectively. One of the roots exceeded 20 mm. in length.

Fourth lower premolar. There is one partly broken representative of this tooth, and it is molariform in type (S17, Pl. XXII, E, F). The crown structure is poorly defined, but seems to be made up largely of two pillars arranged antero-posteriorly. The greatest length of the crown is 16 mm., and the greatest breadth 12 mm. Two roots are disposed antero-posteriorly, and appear to have exceeded 14 mm. in length. The posterior root is partially divided into labial and lingual parts near its tip.

Third lower premolar. Only the remains of the roots of one of these teeth were found, embedded in the fragment of jaw bearing a second and first molar (S17, Pl. XXII, E, F). Two roots appear to be arranged antero-posteriorly, and one of these is estimated to have exceeded 22 mm. in length.

The length of the lower molar series in the type specimen was 120 mm. on the left side and 121 mm. on the right side.

Upper Cheek Teeth

When the upper teeth are compared with the lower teeth, certain differences are sufficiently marked to be summarised as follows: The upper cheek teeth are broader than the lower, and show more complex and folded enamel patterns; the structure of the third upper molars is less regular, and there is a tendency in all the teeth for the arrangement of the columns to be oblique, the columns on the labial side of the tooth being placed slightly in front of the level of their lingual companions (Pls. XXIII and XXIV).

Third upper molars: seven specimens from five individuals. As already mentioned, the crown structure of these teeth is less regular than in the case of the lower third molars (S20, Pl. XXIV, A). The first two, and in some cases three, pairs of lateral pillars can be compared with the corresponding structures in the lower teeth, although they are obliquely placed, with the labial pillars ahead of the lingual partners. At least three regular lateral pillars are found on the lingual side of all the specimens, but there may be only two such regular lateral pillars on the labial side. Behind this regular part of the tooth is found a variable number (5—7) of smaller pillars, irregularly arranged in such a way as to defy division into median and lateral pillars. The posterior extremity of the tooth may consist of a single pillar, or of two pillars of approximately equal size. In the anterior median position is a pillar either frankly divided into a central triangular mass with two

small outriders, one on each side, or showing a clear tendency to be divided in this way. In the 1/2 and 2/3 intervals there is usually a single smaller median pillar; occasionally this is duplicated. A curious feature of the lateral pillars is a groove which appears on the outer side of the pillars low down, near the crown/root junction. This is well seen on the lingual side of the specimen S15 (Pl. XX, B). The third upper molars erupt in much the same way as the corresponding lower teeth (see p. 172).

As in the case of the corresponding lower teeth, the upper third molars have well developed roots along their whole length. The roots supporting the first two lateral pillars are usually separate, and may be divided so that two rootlets support one pillar. Behind this the roots are more or less fused (S4, Pl. XXIV, D), sometimes into plates similar to those seen in the lower teeth. The roots diverge widely when seen end-on, and their general curvature is backwards (S5, Pl. XXIII, B).

Second upper molars: four specimens from three individuals. The fundamental structure of the crown is two pairs of lateral pillars, an anterior median pillar, a single central pillar, and a posterior median pillar. The enamel bounding these pillars is considerably folded and the picture is complicated by the presence of additional small enamel nodules. The maximum number of these is eight, one on each side of the anterior and posterior median pillars and two between each pair of lateral pillars. The disposition of the pillars shows the same slant as is seen in the third molars, with the labial side in advance. The anterior median pillar is situated more or less on the lingual side of the tooth (S20, Pl. XXIV, A). In later wear the posterior median pillar tends to fuse with the posterior lateral pillar on the lingual side (S20, Pl. XXIV, A).

Four roots are present, the posterior pair being larger than the anterior. The general curvature of the roots is backwards (S5, Pl. XXIII, B).

	Dimensions of Crown.						
	Greatest Length.	Greatest Breadth.	Occlusal Breadth.	Height of unworn pillars above root.		Length of Roots.	
				3rd pillar.	Posterior group.	Anterior.	Posterior.
Third Upper Molars							
S4 (R)	65	25	22	29	22	34	25
S5 (L)	64	25	20	36	30	34	22
S10 (R)	67	26	23	—	26	—	—
S11 (L)	70	26	23	—	27	—	—
S14 (R)	70	24	—	32	32	29	—
S15 (L)	70	26	—	36	35	26	—
S20 (L)	63	28	23	—	—	—	—
Second Upper Molars							
S5 (L)	29	22	19			20+	
S7 (R)	29	22	17			29	
S8 (L)	29	22	17			—	
S20 (L)	32	24	22			27+	

Table III: Dimensions of Second and Third Upper Molars in mm.

First upper molars: two specimens from the same individual. As in the case of the corresponding lower teeth, both specimens exhibit advanced wear. Only one of the two is in a sufficiently early stage of wear to allow analysis of the original enamel pattern. Specimen S7 (Pl. XXIII, D) suggests that in early wear a first molar resembles a second, on a smaller scale; as wear advances fusion develops between the anterior median pillar and the two adjacent lateral pillars, and between the central and posterior median pillars and the two posterior lateral pillars. In advanced wear the appearance is of two rather large nondescript enamel figures arranged antero-posteriorly. At this stage there is little difference in the appearance of two rather large nondescript enamel figures arranged antero-posteriorly. At this stage there is little difference in the appearance of the worn surfaces of the upper and lower first molars.

In neither specimen were the roots clearly defined, but there are indications that they are four in number, as in the case of the second molars and the first lower molars.

The greatest length, greatest breadth, and occlusal breadth of the two teeth are 20, 18 and 15 mm. (S7); 21, 20 and 17 mm. (S8), respectively.

Fourth upper premolar (S7, Pl. XXIII, C, D). A single specimen of this tooth was recovered and it is distinctly molariform in appearance. There are two lateral pillars, and an anterior and posterior median complex, each consisting of a reasonably large mass with several additional minute enamel nodules. Greatest length 8 mm., greatest breadth 9 mm., occlusal breadth 8 mm.

There appear to have been two labial roots and one lingual root. The anterior labial root is smaller than the posterior, and is 18 mm. long.

Discussion

There is no difficulty in identifying the genus to which these teeth belong as *Mesochoerus,* first defined by Shaw and Cooke in 1941. These authors listed as diagnostic characters of the third lower molar (type specimen) of this genus a relatively low crown, columns clearly separated from one another, a cingulum demarcating crown from root, and large brachyodont roots. The teeth here described agree with these criteria in each particular.

Apart from the specimen originally named *Notochoerus paiceae* by Broom, to which species Shaw and Cooke referred further material when renaming the genus, only Leakey (1942, 1943) has described additional species of *Mesochoerus.* The first was *Mesochoerus olduvaiensis,* described on two mandibular fragments, each with a third and second molar. These fragments were recovered from Beds I and II at Oldoway, horizons regarded as Middle

Pleistocene. The second was *Mesochoerus heseloni,* described from seven mandibular and two maxillary fragments found at Omo, Abyssinia. Here the fossil beds were stated to be of Lower Pleistocene age.*

The differences between the present species and *M. paiceae* or *M. heseloni* are considerable. *M. heseloni* has third molars which are shorter and lower crowned than in the present species. The two described specimens of M_3 of *M. paiceae* are not only shorter and higher crowned than the specimens described here but are also less complex, having four pairs of lateral columns as against five.

There remains *M. olduvaiensis.* The general structure and appearance of the teeth do not differentiate them from those described by Leakey (1942). There are five pairs of lateral pillars in M_3 and the teeth are not as hypsodont as those of *M. paiceae.* The three specimens of M_2 here described have a well developed anterior median pillar, whereas both teeth described by Leakey lacked this feature. This characteristic of M_2 was included by Leakey in the diagnosis of *M. olduvaiensis,* so that a difference of structure is apparent. Its taxonomic value may, however, be doubted.

It is only when the measurements shown in Table I are examined in detail that the differences between Leakey's and the present species become clear. Despite the length of M_3 which exceeds that of Leakey's species by about 10%, the teeth are on the average 10% narrower. The difference in length/breadth index becomes correspondingly striking (mean of 3.4 against 2.7 in *M. olduvaiensis*). With the increase in length has gone a certain increase in the height of the crown so that the length/height index does not differ markedly.

It is clear that these measurements must be held to differentiate the present species from *M. olduvaiensis.* The name *Mesochoerus lategani* is suggested in honour of Mr. S. P. Lategan, on whose farm the specimens were discovered.

The upper cheek teeth of *M. olduvaiensis* have not been recorded. It is of interest to see that the posterior part of the upper third molars described here show the same irregularity of structure as is found in the upper third molars of *Mesochoerus heseloni.* On the other hand neither Leakey's (1943) nor Arambourg's (1947) illustrations of the occlusal surface of the upper third molar of *M. heseloni* show any trace of the obliquity in the arrangement of the pillars which is so characteristic of the upper teeth found at Hopefield (Pls. XXIII and XXIV).

The geological period to which these fossil specimens should be referred is difficult to determine, but the total faunal assemblage from Hopefield

* Arambourg (1947) allots this species to the genus *Omochoerus* which he created, and argues that the genus *Mesochoerus* may have to be merged with *Hylochoerus.*

suggests an early Upper Pleistocene period. The possibility that specimens of a Middle Pleistocene period have been mingled with later material cannot at this stage be altogether excluded. The results of fluorine estimations on a wide range of specimens do not so far support the idea that fossil remains of widely differing age have been confused by sand movement on the site. Leakey (1953) comments that in East Africa no specimens of *Mesochoerus* have been recovered from Upper Pleistocene deposits, and that if the evidence for an Upper Pleistocene dating at Hopefield is correct, the presence of the *Mesochoerus* represents survival of a genus which had become extinct further north. It is also noteworthy that the *Mesochoerus* teeth and jaws are the only suid specimens so far recovered from the site, which again suggests the late survival of an isolated species.

SUMMARY

Fossil Hippopotamus and suid remains from Hopefield are described. The single suid species represented is named *Mesochoerus lategani* sp. nov. The early Upper Pleistocene age which must provisionally be attached to the specimens is contrasted with the Middle Pleistocene date allotted to the type specimens of *M. olduvaiensis*, and the Lower Pleistocene dating of *M. heseloni*.

ACKNOWLEDGEMENTS

We are indebted to Dr. H. B. S. Cooke, University of the Witwatersrand, for generous advice and assistance. Mr. G. McManus, Surgery Department, University of Cape Town, kindly photographed the specimens.

The University of Cape Town is grateful to three donors who wish to remain anonymous and who sponsored the work at Hopefield.

Publication of this paper was assisted by a grant-in-aid made by the Council of the University of Cape Town.

REFERENCES

Arambourg, C. 1947. Mission Scientifique de L'Omo, Tome I, Fascicule III: Paléontologie.

Cooke, H. B. S. 1949. The Fossil Suina of South Africa, Trans. Roy. Soc. S. Africa, *32*, 1-44.

Drennan, M. R. 1953. A preliminary note on the Saldanha skull, S.A. J. Sci., *50*, 7-11.

Leakey, L. S. B. 1942. Fossil Suidae from Oldoway, Journal of the East African Natural History Society, *16*, 178-196.

Leakey, L. S. B. 1943. New fossil Suidae from Shungura, Omo, Journal of the East African Natural History Society, *17*, 45-61.

Leakey, L. S. B. 1953. Personal communication.

Middleton-Shaw, J. C. and Cooke, H. B. S. 1941. New Fossil Pig remains from the Vaal River Gravels, Trans. Roy. Soc., S. Africa, *28*, 293-299.

Simpson, G. G. 1945. The Principles of Classification and a Classification of Mammals, Bull. Am. Mus. Nat. History, *85*, 1-350.

Singer, R. 1954. The Saldanha Skull from Hopefield, South Africa. Amer. J. Phys. Anthrop., September (in the press).

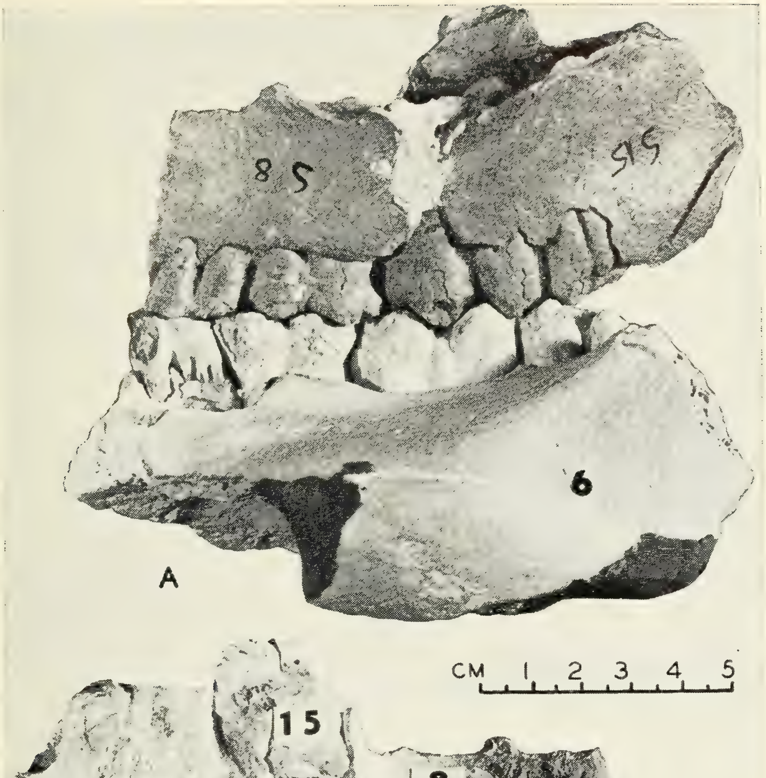


Plate XX. A. Labial (lateral) view of the left upper and lower jaw fragments of the type specimen, in occlusion (S6, S8, S15). B. Lingual (medial) view of the same.

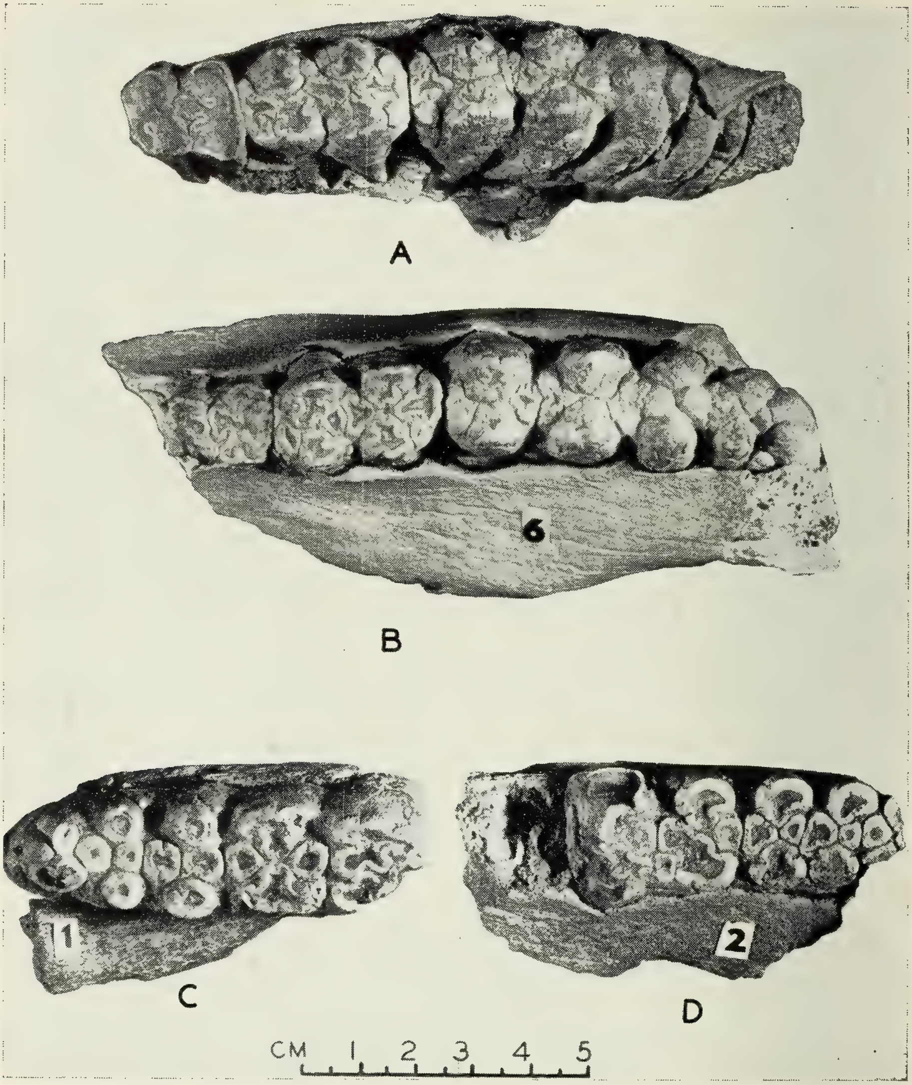


Plate XXI. A, B. Occlusal views of type specimens shown in Plate XIX (S8 + S15 upper, S6 lower). C, D. Occlusal views of right (S1) and left (S2) lower third molars. S2 is in more advanced wear and is broken posteriorly.

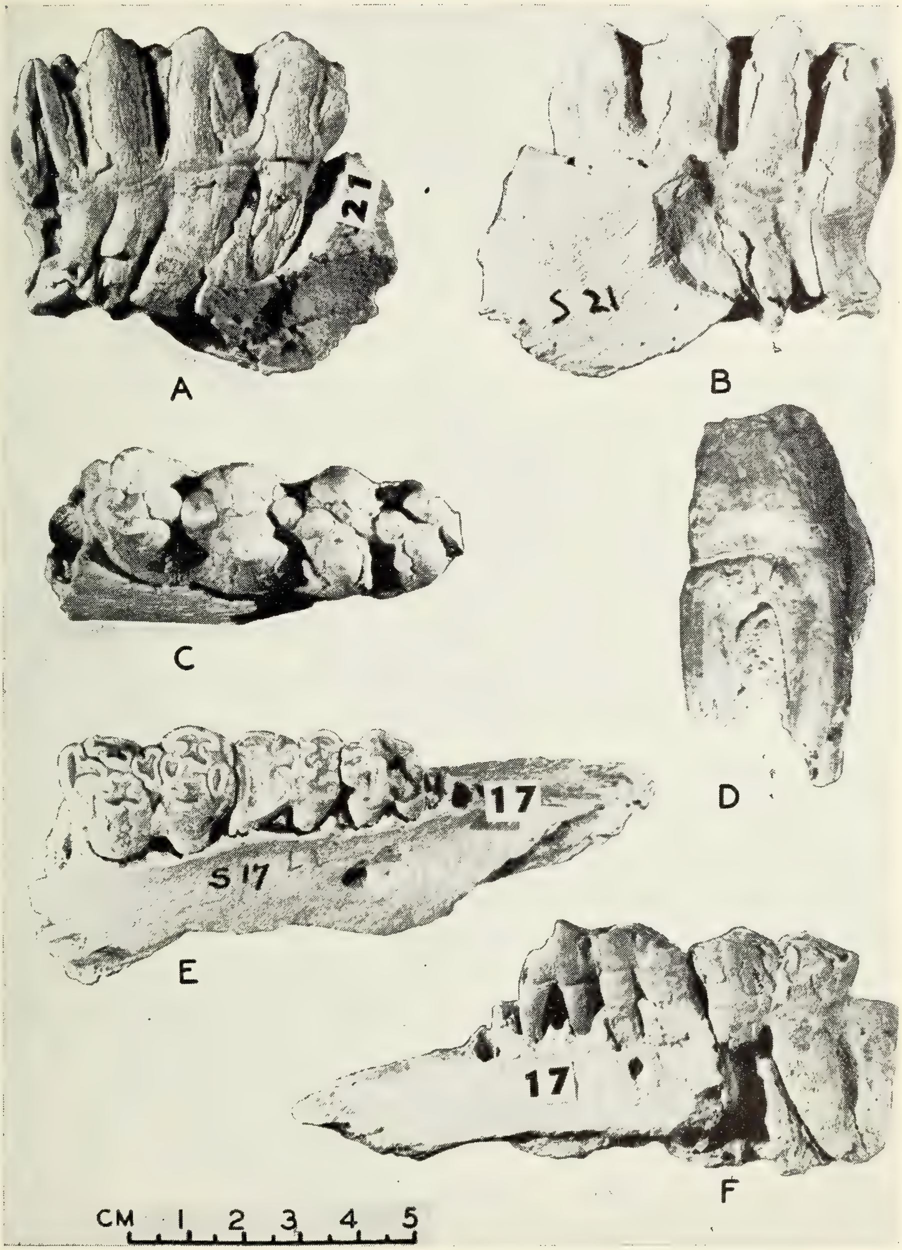


Plate XXII. A, B, C. Lingual, labial and occlusal views, respectively, of right lower third molar. D. Anterior view of right lower third molar (S16). E, F. Occlusal and lingual views, respectively, of right lower second molar, first molar, and fourth premolar (S17).

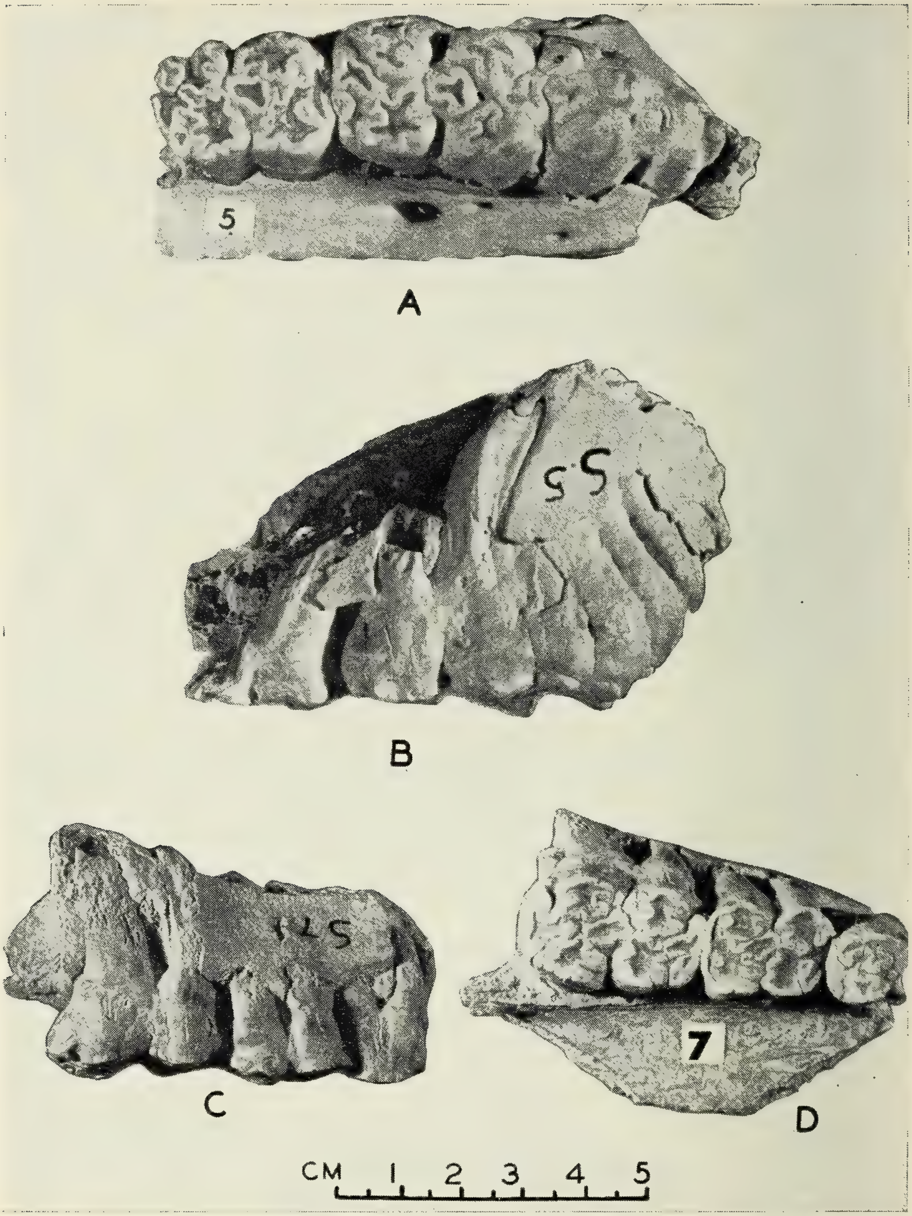


Plate XXIII. A, B. Occlusal and labial views, respectively, of left upper third and second molars (S5). C, D. Labial and occlusal views, respectively, of right upper second molar, first molar, and fourth premolar (S7).

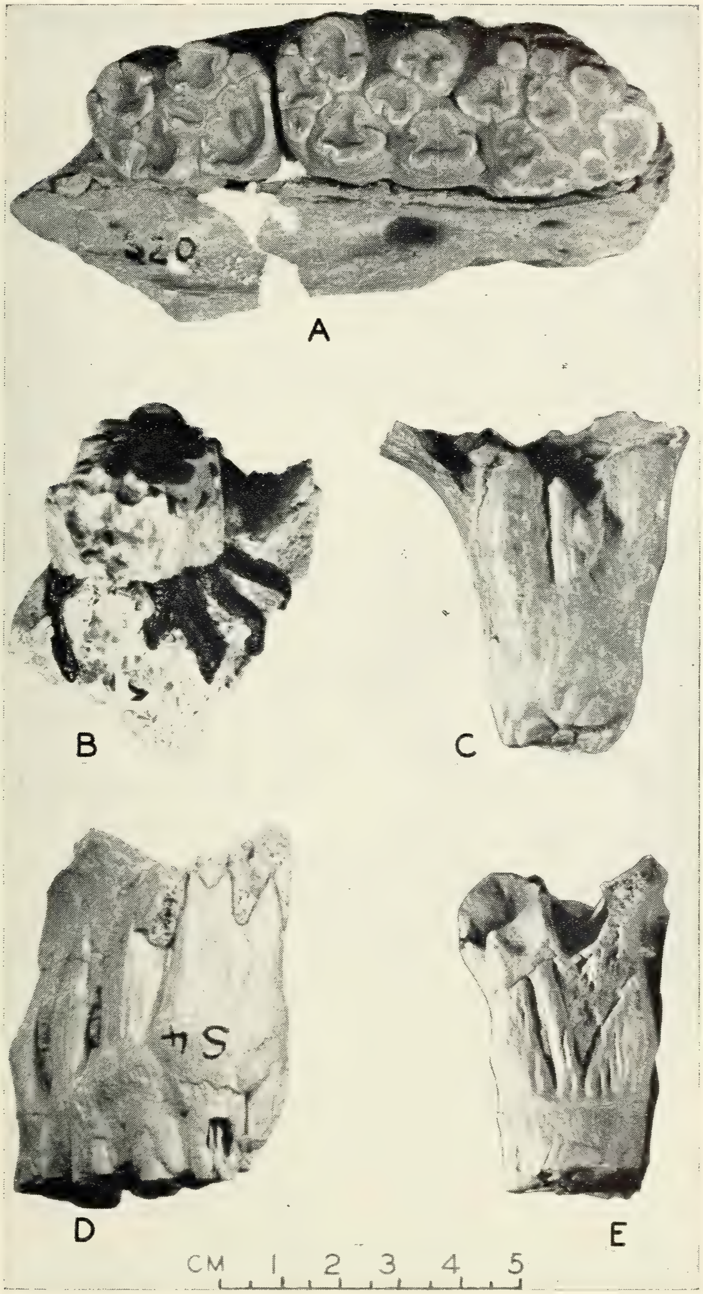


Plate XXIV. A. Occlusal view of left upper third and second molars (S20). B. Posterior view of left lower third molar (S9) to show deformity of roots which have been painted black. C. Anterior view of right upper third molar (S14). D. Oblique posterior view of right upper third molar (S4). E. Anterior view of right upper third molar (S4).

L. D. BOONSTRA, D.Sc.

Struthiocephalellus: A new Deinocephalian

The Girdles and Limbs of the South African Deinocephalia

13. *Struthiocephalellus:* A New Deinocephalian. By Lieuwe Dirk Boonstra, D.Sc.

(With 3 text-figures.)

In the collection of the South African Museum there is a specimen (S.A.M. 5006) collected by Haughton in 1916 on Abrahamskraal, Prince Albert, which according to Rossouw (4) is Low *Tapinocephalus* zone. This specimen consists of much of the skeleton of a small Tapinocephalian. There is preserved: much of a distorted and weathered skull in two parts, viz. a maxillary and an occipital part not in contact; parts of the vertebral column, part of a scapula, most of a humerus, the proximal end of an ulna; the greater part of a distorted pelvis, a femur and the proximal end of a tibia, together with other fragments.

The bones of the girdles and limbs are being described in a forthcoming paper on these elements based on all the Deinocephalian material in the Museum.

The skull (Figs. 1-2) is about half the size of that of *Struthiocephalus whaitsi*. The pachyostosis is weak so that the postorbital bar is relatively slender and the posttemporal opening roomy. The occiput is fairly upright and the quadrate not shifted very far anteriorly. The snout is moderately high.

Owing to the distortion and the lack of contact between the maxillary and occipital pieces the two figures I give here are reconstructions and represent orthoprojections of the dorsal and ventral surfaces projected on to the plane in which the alveolar borders of the maxillaries lie.

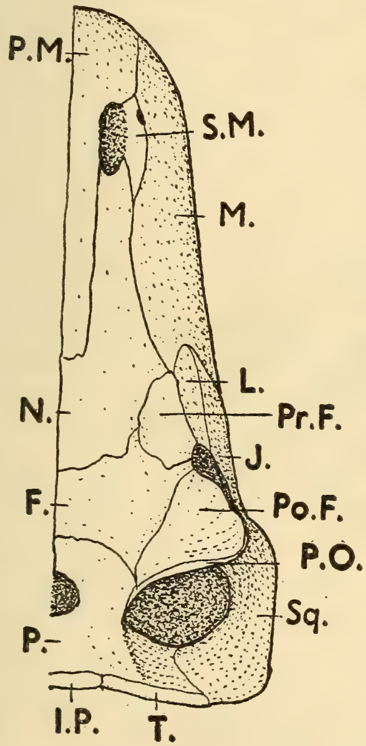
A comparison of these figures with those given for *Struthiocephalus whaitsi* (2) shows that the present skull, apart from its being only a half as large, is very similar in general structure. The chief points of difference are: Little pachyostosis, no fronto-nasal boss, slender postorbital bar, more upright occiput and less forward displacement of the quadrate.

These points of difference might very well be thought to merely indicate juvenility in the present skull. However, in our collection I (2) have described a juvenile skull (S.A.M. 11493) of *Struthiocephalus whaitsi* which is just as long as that of two adult skulls, but its youth is indicated by the fact that the teeth are just beginning to erupt. Now in the present skull (S.A.M. 5006) there is a full set of sixteen teeth which would tend to show that although so much smaller it cannot be younger than the juvenile skull (S.A.M. 11493) of *Struthiocephalus*.

Unfortunately no crowns of any of the anterior teeth are preserved, but judging from the nature of the roots it does not appear probable that in the

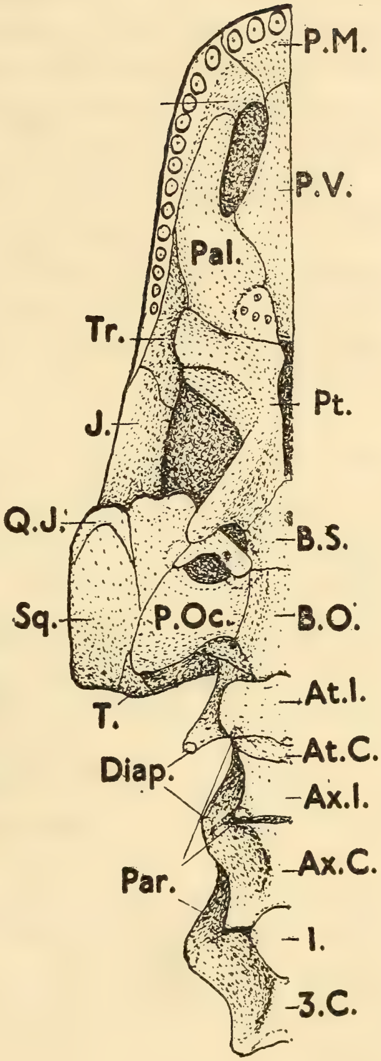
anterior teeth the crowns had the usual Tapinocephalian structure consisting of talon and horse-shoe-shaped attrition surface, but rather that they were simple pointed teeth.

Fig. 1.



Dorsal aspect of the skull of *Struthiocephalellus parvus*. S.A.M. 5006. Abrahamskraal, Prince Albert. (× ⅓.) This as well as Fig. 2, is a reconstructed projection by pantograph on to the plane in which the maxillary alveolar borders lie. F.—frontal; I.P.—interparietal; J.—jugal; L.—lacrimal; M.—maxilla; N.—nasal; P. — parietal; Po.F. — postfrontal; Pr.F.—prefrontal; P.M.—premaxilla; P.O. — postorbital; S.M. — septomaxilla; Sq.—squamosal; T.—tabular.

Fig. 2.



Ventral aspect of the skull and the first three cervicals of *Struthiocephalellus parvus*. (× ⅓.) At.C.—atlantal centrum; At.I.—atlantal intercentrum; Ax.C.—axial centrum; Ax.I.—axial intercentrum; B.O. — basioccipital; B.S.—basisphenoid; Diap.—diapophysis; I.—third intercentrum; Pal.—palatine; Par.—parapophysis; P.Oc.—paroccipital; Pt.—pterygoid; P.V.—prevomer (vomer); Q.—quadrate; Q.J.—quadratojugal; Tr.—transversum; 3 C.—centrum of third vertebra.

The crowns in some of the posterior teeth are imperfectly preserved. Here the crowns appear spatulate in outline and labio-lingually compressed. In one or two of the rear crowns there appears to have been a stronger central cusp with a weaker posterior and anterior cusp, strongly reminiscent of those known in *Agnosaurus* (1) and the Russian *Rhopalodon*.

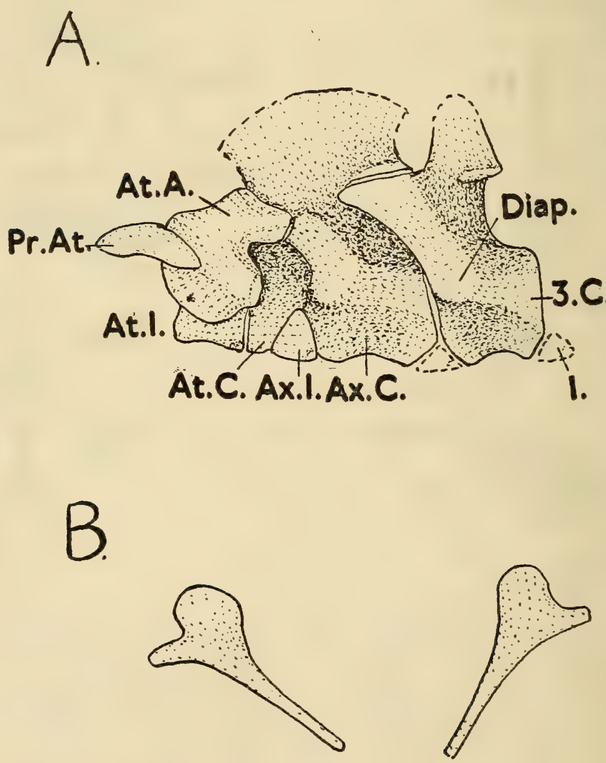
In view of the condition in *Agnosaurus* the possibility that the spatulate rear teeth may represent "milk" teeth cannot be excluded.

A series of three cervical vertebrae is preserved in articulation with the occipital condyle.

The cervical vertebrae (Figs. 2 and 3) are very similar to those of *Moschops* and *Mochognathus* (3) and to those of the Synapsids generally.

The proatlas is a stout bone; in lateral view its outline is that of a shallow segment; anteriorly it has a ventral facet for articulation with the

Fig. 3.



A. Lateral view of the first three cervical vertebrae of *Struthiocephalellus parvus*. (× ⅓.) At.A.—atlantal arch; Pr.At.—proatlas.
B. Lateral view of left and right atlantal ribs. (× ⅓.)

exoccipital and a similar facet posteriorly articulates with the atlantal prezygapophysis.

The atlas is temnospondylous with a paired neural arch resting on a large atlantal intercentrum and an odontoid-like pleurocentrum. The arch is of complex shape; dorso-posteriorly a postzygapophysis articulates with the prezygapophysis of the axis; dorso-anteriorly a prezygapophysis gives articulation to the proatlas; postero-laterally there is a strong diapophysial process carrying a facet for the articulation of the tuberculum of the atlantal rib; near its antero-ventral edge there is a small vertebrarterialis foramen; dorsally the two halves do not meet to form a spine.

The atlantal intercentrum is large; it carries a posteriorly directed parapophysial facet on its postero-lateral edge for the capitulum of the atlantal rib.

The atlantal pleurocentrum is mostly covered by the atlantal rib, but is probably as that described in *Moschops* and *Mochognathus*.

The axis has the two halves of the neural arch fused to each other and to the pleurocentrum to form a typical holospondylous vertebra.

The spine is comb-shaped; anteriorly an upwardly directed prezygapophysial facet articulates with the postzygapophysis of the atlantal arch; postero-dorsally horizontal upwardly facing postzygapophyses articulate with the prezygapophysis of the succeeding vertebra; well below the junction of arch and centrum there is situated a strong process carrying the diapophysial facet for the tuberculum of the axial rib, whose capitulum articulates with a parapophysial facet situated on the postero-lateral corner of the axial intercentrum.

The axial centrum is laterally excavated below the diapophysis and ventrally has a sharp keel.

The third intercentrum is smaller than its predecessors.

The third cervical has a bluntly pointed spine and its centrum is deeply excavated below the diapophysis so that ventrally it shows a sharp keel.

The atlantal rib (Fig. 3 B) is preserved on both sides; it is a greatly flattened small bone with a weak shaft, a greatly expanded leaflike tuberculum and a much weaker capitulum.

This specimen in size comes very near to *Moschosaurus* and *Agnosaurus* and agrees with these two forms in having the pachyostosis little developed, the quadrate not greatly forwardly displaced and the skull height not greatly reduced. In the structure of its palate and the dorsal cranial surface it shows considerable similarity to the much larger *Struthiocephalus* from which it differs however in the nature of its dentition and in the structure of the girdles and limb-bones.

For this form I propose the name—

Struthiocephalellus parvus. Gen. et Sp. Nov. Holotype: S.A.M. 5006. Skull, vertebrae, girdle- and limb-bones. Abrahamskraal, Prince Albert. Low *Tapinocephalus* zone.

REFERENCES

1. Boonstra, L. D. *Agnosaurus* Gen. Nov.: 'n Nuwe Geslag van die Deinocephaliërs. Tydsk. Wet. Kuns. 12, 2, 242-245. 1952.
2. Boonstra, L. D. The Cranial Morphology and Taxonomy of the Tapinocephalid genus *Struthiocephalus*. Ann. S. Afr. Mus. 42, 1, 32-53. 1953.
3. Gregory, W. K. The Skeleton of *Moschops capensis* Broom, a Dinocephalian from the Permian of South Africa. Bull. Amer. Mus. Nat. Hist. 61, 179-251. 1926.
4. Rossouw, P. J. en de Villiers, J. Die Geologie van die Gebied Merweville, Kaapprovinsie. Toel. Blad. 198. Geol. Opname, Unie S. Afr., 1-71. 1952.

14. *The Girdles and Limbs of the South African Deinocephalia.* By Lieuwe Dirk Boonstra, D.Sc.

(With 6 diagrams, 108 text-figures and Plate XXV.)

1. Introduction

In this communication I intend describing the pectoral and pelvic girdles and the fore- and hind-limbs of the large number of Deinocephalian specimens housed in the South African Museum in Cape Town. The nature of the material determines the method of treatment, which will in this case have to assume, in the taxonomic part, the form of an illustrated catalogue.

In all, the Museum Register contains 106 separate specimens in which some part or other of the girdles or limb-bones is preserved. In a very large number of cases these postcranial elements are not associated with any cranial material and identification is thus rendered difficult in view of the fact that authors in the past have usually made skulls and jaws "types". Moreover, in many cases the specimens consist of isolated individual bones which, being unassociated with other elements of the postcranial skeleton, makes the task of identification no easier.

All the specimens were collected in the *Tapinocephalus* zone of the Lower Beaufort; nearly all in the area known as the Koup, which includes parts of the districts Beaufort West, Prince Albert and Laingsburg, with only a couple from the area north of the Nieueveld Escarpment in the districts of Sutherland and Fraserburg.

Rossouw (26) has recently subdivided the *Tapinocephalus* zone into three subdivisions, and it is of interest to record that the specimens to be described here come mostly from the lower subdivision.

Since the Museum's first acquisition in 1904 the following collectors have contributed to the collection of Deinocephalian girdle- and limb-bones: Cloete, Oakley, le Roux, du Plessis, Cairncross, Maddison, Whaits, Haughton, van der Byl, Boonstra, Avenant and Marais. Of these, Haughton with 18 and Boonstra with 65 specimens are the more important collectors.

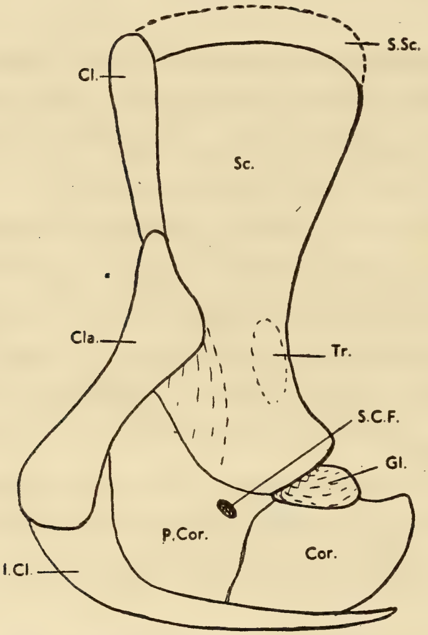
2. Historical and Morphological

A. *The Pectoral Girdle* (Diagram 1)

In 1889 Seeley (28) figured a coracoid and incorrectly interpreted it as the pubis of *Titanosuchus*. Broom (8) in 1905 mentioned parts of the shoulder

girdle of *Pelosuchus*. In 1914 Watson (29) figured the scapulocoracoid of *Phocosaurus* and described the scapula, coracoid and cleithrum of *Titanosuchus*. In the same year Broom (11) figured and described the shoulder girdle of *Moschops*, and on the same material Gregory and Camp (17), Romer (25) and Gregory (18) based their figures and descriptions. In 1914 Broom (10) also published a photograph of a Titanosuchian pectoral girdle (A.M.N.H. 5611) under the name *Tapinocephalus atherstonei* in error, and this scapulocoracoid was later figured by Gregory (18) under the name "*Tapinocephalus*" to indicate his lack of confidence in Broom's identification. In 1915 the pectoral girdle of *Struthiocephalus* was shown in Haughton's (20) photograph of the mounted specimen in the South African Museum. Broom (14) in 1929 figured and described the pectoral girdle of *Jonkeria truculenta*. In 1931 von Huene (21) figured an interclavicle, which he thought was that of a Titanosuchid. In 1940 Byrne (16) described and figured parts of the girdle of *Moschoides*. Although pectoral elements are mentioned in connection with some of the other described Deinocephalians, they were neither figured nor described.

Diag. 1.



Semi-diagrammatic sketch of a Titanosuchian pectoral girdle in lateral view. Cl.—cleithrum; Cla.—clavicula; Cor.—coracoid; Gl.—glenoid; I.Cl.—interclavicula; P.Cor.—precoracoid; Sc.—scapula; S.C.F.—foramen supracoracoideus; S.Sc.—suprascapula; Tr.—mound, ridge or tubercle from which the scapular head of the m. triceps originates.

In the South African Museum collection the pectoral girdle is well represented. The scapula is preserved wholly or in part in 36 specimens, the coracoid in 16, the precoracoid in 12, the interclavicle in 15, the clavicle in 5, whereas the cleithrum is only preserved incompletely in 1 specimen.

The Deinocephalian pectoral girdle is composed of 11 bones — one unpaired bone and five pairs — as is the case in all primitive reptiles. These are the interclavicula, a pair of scapulae, coracoids, precoracoids, cleithra and claviculae. With which in life a cartilaginous sternum was probably associated. These eleven bones together form a U-shaped framework encasing the thorax and is supported semi-slung by the paired fore-limbs.

Ventrally the interclavicle, bisected by the median line, forms the connecting link between the two limbs of the U. Each limb is formed by the more or less vertically disposed scapulo-coracoid, which consists of a dorsal bladelike scapula and a ventral, antero-posteriorly elongated, coracoidal plate formed by the large precoracoid and a smaller coracoid. The lower edge of the coracoidal plate rests on the stem of the interclavicle, which sometimes carries a strong median ridge against which the coracoids abut.

On the posterior surface of the scapulo-coracoid, at the junction of the scapula and the coracoid, lies the simple, antero-posteriorly shortened, glenoid cavity, which receives the shortened oval head of the humerus. The glenoid has a dorsal facet lying in the scapula and this faces ventro-posteriorly but sometimes also slightly externally, and a ventral facet on the coracoid facing dorso-posteriorly and also much externally. The nature of the glenoid cavity makes the humerus lie with its distal end somewhat or fairly much lower than its proximal end. Moreover, it limits the anterior disposition of the humerus.

On the posterior border of the scapula, some distance above the glenoid, lies a mound, or ridge or a prominent tubercle, from which the scapular head of the triceps originates. Along its anterior border the scapula is flanked by the elongated cleithrum, which in the Tapinocephalia is, where known, a rudimentary splintlike bone, but in the Titanosuchia is still functional as a fairly strong elongated element with a spatulate dorsal end projecting above the upper edge of the scapula, to which a cartilaginous suprascapula was attached in life. Below the cleithrum and lying along the anterior edge of the scapula and precoracoid is the long platelike clavicle, which in the Titanosuchia, and to a lesser extent in the other forms, dorsally overlaps the lower end of the stem of the cleithrum, fitting into a groove in this bone. In all the Deinocephalia the clavicle, where known, has its widely spatulate ventral end clasping the upturned antero-lateral external surface of the interclavicle, which develops a more or less deep groove for the reception of the clavicle.

In the pectoral girdle the two coracoids and the scapula are more or less firmly joined by sutures to each other, with the other elements, the dermal bones, more loosely applied to them. Ridges and grooves limit the movements of the elements *inter se* and strong ligaments holding them together allow a fair amount of movement. There is considerable freedom of movement between the two halves allowing for difference of disposition when one fore-limb is disposed anteriorly and the other posteriorly.

As a whole the pectoral girdle is thus a massive structure of overlapping and supporting bones, united by suture or ligament, forming a strong but

The girdle is strongest in the Titanosuchia, where quick forceful movements are requisite for their carnivorous habits, weaker in the Tapinocephalia, whose habits were more leisurely and more aquatic, and in the Anteosauria it is weak, with the distinctive tricipital tubercle on the scapula, and a more crawling habit.

The Deinocephalian pectoral girdle shows definite advances beyond the morphological stage achieved by the Pelycosaurs. The more important advances are: the loss of the supraglenoid buttress and the supraglenoid foramen and the development in its stead of a mound, or ridge, or tubercle for the insertion of the scapular head of the triceps muscle; the antero-posterior shortening of the glenoid cavity, entailing the loss of the intricate "screw-shape" and the formation of a simple glenoid with a dorsal facet on the scapula and a ventral facet on the coracoid, and the glenoid, as a whole, facing ventro-postero-externally; the total exclusion of the precoracoid from the articulation in most forms, whereas in the others it forms no more than a small part of the anterior rim of the glenoid; the reduction in size and functional importance of the cleithrum (greatest in the Tapinocephalia, least in the Titanosuchia and probably also in the Anteosauria); the increase in size of the precoracoid, particularly antero-dorsally for the m. supracoracoideus, and concomitantly an extension of the area for the origin of the m. scapulo-humeralis; the loss of the dorsal process of the coracoid from which the coracoidal head of the triceps originated primitively; the development of a very strong interclavicle with a strong spatulate anterior end bent sharply upwards; the clavicle is a flat bone of considerable size.

The Deinocephalian pectoral girdle is less advanced than that of some of the higher Therapsids in that: no acromion is developed and there is no indication of the development of an incipient spina scapularis.

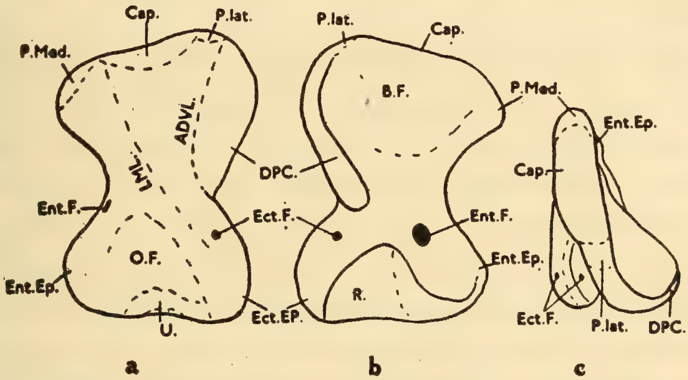
B. *The Fore-limb* (Diagrams 2 and 3)

Humerus

The first Deinocephalian humerus to be figured was one from Varsfontein, which Owen (23) in error referred to *Pareiasaurus,* and Lydekker (22) provisionally included in *Tapinocephalus.* In 1889 Seeley (28) figured a specimen from Koedoeskop as that of *Titanosuchus,* since it was said to be associated with the type skull fragments. Broom (7) in his description of *Scapanodon* mentions three humeri as possibly associated with the jaw fragments, but does not figure them. Then in 1909 Broom (9) made a humerus the type of *Eccasaurus priscus* and erroneously stated that it was from the Ecca Beds, whereas in fact, the farm Sandvlakte has outcrops of the *Tapinocephalus* zone of the Lower Beaufort Beds. *Eccasaurus* was

finally by Broom (15) considered to be one of the herbivorous Tapinocephalia, whereas, as will appear later, it is one of the carnivorous Anteosauria. In 1914 Broom (11) figured the humerus of *Moschops* and published (10) a

Diag. 2.



Semi-diagrammatic sketch of a Jonkerid humerus. a. Dorsal view. b. Ventral view. c. Proximal view. A.D.V.L.—anterior dorso-ventral line; B.F.—bicipital fossa; Cap.—caput humeralis; D.P.C.—delto-pectoral crest; Ect.Ep.—ectepicondyle (radial); Ect.F. — ectepicondylar foramen; Ent.Ep. — entepicondyle (ulnar); Ent.F.—entepicondylar foramen; L.M.L.—latero-medial line (separates the proximal and distal dorsal surfaces of the humerus); O.F.—fossa for the olecranon; P.Lat.—processus lateralis; P.Med.—processus medialis; R.—radial condyle or capitellum; U.—ulnar condyle.

photograph of the fore-limb of a Titanosuchian, which was erroneously referred to *Tapinocephalus atherstonei*. This humerus was subsequently figured by Gregory (18) without the ectepicondylar foramen being indicated. I located this foramen when at the American Museum in 1935 thus proving it to be Titanosuchian and not Tapinocephalian. In 1914 Watson (29), reviewing the Deinocephalian material in the British Museum (N.H.), figured an imperfect humerus of *Pnigalion oweni*, and also located an ent- and ect-epicondylar foramen in Seeley's humerus of *Titanosuchus*. The humerus of *Struthiocephalus* is poorly shown in Haughton's (20) photograph and Broom's (15) reconstruction. In his comparative study Romer (25) figured the humerus of *Moschops*, as did Gregory (18). In 1928 Broom (13), discussing the confusion with regard to the British Museum material, figured a humerus, which he regarded as that of *Tapinocephalus atherstonei*, whereas, having two epicondylar foramina, it must be that of some Titanosuchian. The following year Broom (14) figured the humerus of *Jonkeria crassus* and briefly described, without a figure, a humerus identified as *Jonkeria* sp. and gave photographs of the humerus of *Dinosphageus* (= *Jonkeria*) *haughtoni*,

and stated that there is a humerus associated with the type skull of *Jonkeria pugnax*. Von Huene (21) figured a humerus identified simply as Deinocephalian, but clearly belonging to the genus *Jonkeria*. Finally Byrne (16) figured the humerus of *Moschoides*.

In the collection of the South African Museum 35 specimens have the humerus adequately preserved and a number where only unsatisfactory ends are preserved.

The humerus in the three divisions of the Deinocephalia, where it is known (Tapinocephalia, Titanosuchia, Anteosauria), shows certain distinctive characters but these are overshadowed by the features they have in common.

The Deinocephalian humerus is a fairly to very short bone, massive in the majority of forms, with greatly expanded ends and a short to very short, strong to very strong shaft. The proximal and distal expansions make an angle relative to each other because of a twisting on the shaft. The amount of this "twist" varies from about 10° to over 40°, but the usual twist is about 15-25° and postmorten deformation usually accounts for the extremes.

The proximal surface of the humerus has in its median part the caput humeralis, which is oval in outline — sometimes narrowly and in other cases broadly oval. Its edges overhang the dorsal and ventral faces of the humerus to a varying degree. The face of the caput is only slightly convex, and, in life, it must have had a thick cartilaginous pad in order to fit the glenoid and make a relatively efficient shoulder joint. Postaxially the caput merges into the processus medialis, which in the Tapinocephalia and Anteosauria lies in about the same plane as the caput, but in the Titanosuchia the processus medialis lies in a plane slightly (Titanosuchidae) or much (Jonkeridea) distally of that in which the caput lies. Preaxially the caput flows into the processus lateralis, which in its turn is distally continued as the deltopectoral crest (D.P.C.). The processus lateralis usually forms the most proximal corner of the humerus and it limits the anterior disposition of the limb.

The distal end of the humerus differs considerably in the Tapinocephalia and Anteosauria on the one hand and the Titanosuchia on the other hand. In the former the capitellum or radial condyle is weak, not sharply modelled, transversely elongate and with little ventral swelling and its face does not extend in proximal direction along the ventral face of the bone; it is thus more distally situated and directed. Whereas in the Titanosuchia the capitellum is strongly bulbous, rounded and it extends moderately to very far proximally along the ventral face, in some cases right up to the plane in which the entepicondylar foramen has its ventral opening; its modelling is strong with sharp and prominent edges in some specimens; thus, although extending to the distal end of the bone, the capitellum is more ventrally situated and directed. The ulnar condyle is relatively weak and not

distinctly demarcated from the radial condyle and its mostly rounded but sometimes slightly trochlear surface lies distally and only just extends on to the dorsal surface; with, in some cases, a shallow trochlear fossa on the dorsal surface to receive the olecranon of the ulna when the epipodial is semi-extended.

Neither of the two epicondyles stretch distally of the articulatory surfaces. In distal view both epicondylar ends are very little thickened in the Tapinocephalia and Anteosauria, whereas in the Titanosuchia they are thick to very thick, indicating an important difference in the development of the flexors, extensors and supinators.

The proximo-dorsal surface is roughly triangular in outline, with the base situated proximally and the apex merging into the dorsal surface of the shaft. This surface is divided by the anterior dorso-ventral line (A.D.V.L.) into two parts. Anteriorly (preaxially) to this line lies the triangular upper face formed by the strong development of the delto-pectoral crest (D.P.C.). This large area (greatest in the Titanosuchia) is indicative of the presence of a very strong m. deltoideus. The ventro-distal corner of the delto-pectoral crest, to which was inserted the m. pectoralis, lies much further distally in the Jonkeridae than in the Tapinocephalia and, in particular, the Anteosauria. Both m. deltoideus and m. pectoralis were apparently much stronger in both groups of the Titanosuchia than in the Tapinocephalia and Anteosauria.

On the other part of the proximo-dorsal surface there lies the fairly weak oblique latero-medial line (L.M.L.), which is strongest in the Titanosuchia. The separate muscle-scars for the scapulo-humeralis, latissimus dorsi and the triceps on this surface are usually not clearly demarcated. But in the plane of the shaft a thickening on the L.M.L. is developed for the attachment of the lateral humeral head of the triceps and in some Titanosuchians a strong moundlike tubercle is developed here.

The dorso-distal surface is also roughly triangular with the apex directed proximally and dying out on the surface of the shaft. Distally this surface is moderately to very greatly expanded by the development of the two epicondylar flanges. Proximal to the distal edge of the bone, formed by the edge of the radial and ulnar condyles, there is a shallow triangular depression lying between the dorsal surfaces of the two epicondylar flanges. The anterior (preaxial) border of this hollow is sharper than the posterior (postaxial) border and is a continuation of the L.M.L. Anterior to this ridge lies the confluent ectepicondylar (radial epicondyle) and supinator flange, which in the Titanosuchia is pierced by the rounded ectepicondylar foramen, either vertically or obliquely. Distally this flange has a thickened truncated end, to which the extensor muscles were attached. The supinator part of this flange has a thin, sharp edge — thinner in the Tapinocephalia and Anteosauria than in the Titanosuchia. In the Titanosuchia the ectepicondylar

foramen pierces this flange either quite near its edge where it is thinnest, or deeper in through much thicker bone. In the first case the perforation is at right angles to the surface, whereas in the latter case the perforation is oblique, with the ventral exit situated further distally than the dorsal entry.

The entepicondylar flange is thicker than the confluent supinator and ectepicondylar flange. To its thick truncated distal end the strong flexors were attached. The slitlike entry of the entepicondylar foramen really lies somewhat proximal to the epicondylar flange proper on the dorso-postaxial or the postaxial surface of the shaft. The foramen perforates the bone obliquely so that its ventral exit lies further distally as well as ventrally.

The proximo-ventral surface of the humerus consists of a large hollowed out triangular surface (the bicipital fossa), which is bounded anteriorly by the large delto-pectoral crest, the proximal edge, formed by the processus lateralis, the caput humeralis and the processus medialis, and posteriorly by the thick posterior edge, to which the median head of the triceps was attached. In this view the delto-pectoral crest is seen to extend ventrally, from its origin at the processus lateralis, as an inclined strong sheet of bone terminating ventro-distally in the thickened corner for the insertion of the m. pectoralis. The pectoralis-corner is never knoblike as in the Pareiasaurs, but is thicker in the Titanosuchia than in the Tapinocephalia and Anteosauria. In *Jonkeria parva* the D.P.C. is particularly massive and short. In the Titanosuchia, with one exception, the pectoralis-corner is situated very far distally, whereas in the Tapinocephalia its distal extension is moderate to small, and in the Anteosauria small. From this corner the pectoral crest subsides into the surface of the shaft in postero-distal direction, abruptly in the Titanosuchia, but gently in the case of the Tapinocephalia and the Anteosauria.

The ventro-distal surface of the humerus is broad to very broad and consists chiefly of the capitellum or radial condyle which is large and massive in the Titanosuchia, but in the Tapinocephalia and Anteosauria it is a much smaller feature. The capitellum lies mostly in the pre-axial half of the distal surface and in the Titanosuchia it forms a large bulbous mass of bone stretching far to very far in proximal direction nearly to or even beyond the plane in which the entepicondylar foramen lies. It is well modelled with sharp borders in the Titanosuchia, whereas in the Tapinocephalia and Anteosauria the modelling is weaker and it is not bulbously swollen and never stretches far in proximal direction. The ulnar articulatory surface is not clearly demarcated from the radial condyle and simply forms the rounded part of the distal edge of the humerus. The lateral portions of the ventro-distal surface form the under surfaces of the ect- and entepicondylar flanges. The ectepicondylar flange is thin and has its edge bent downwards. In the Tapinocephalia and Anteosauria its upper end is separated from the surface of the shaft by a groove, and it is, in the absence of the ectepicondylar

foramen in these groups, along this groove that the radial nerve ran. The entepicondylar flange is thick. The ventral opening of the entepicondylar foramen, through which passed the medial artery and nerve, is in the Tapinocephalia and Anteosauria a fairly narrow slit, but it is more oval in the Titanosuchia. In the Tapinocephalia and Anteosauria the entepicondylar foramen is always a considerable distance from the proximal edge of the radial condyle, whereas in the Titanosuchia the radial condyle in some forms extends so far in proximal direction that the foramen lies close to the proximo-postaxial edge of the condyle.

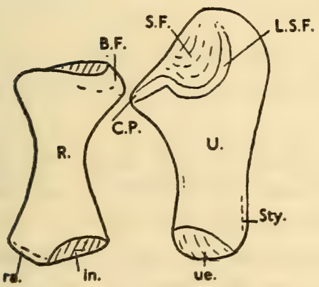
The Shoulder Joint

From the description of the glenoid cavity and the shape of the caput humeralis it is clear that the shoulder joint was not a very efficient structure. A large amount of cartilage and strong ligaments were necessary to make the joint function at all well. Even so, any great forward disposition of the humerus must have taken the head of the humerus out of the socket. It would appear that in the Titanosuchia the humerus lay more horizontally than in the Tapinocephalia, where it was inclined obliquely downward towards the elbow.

Radius

The radius is not very well known. In this collection only 7 good radii are preserved. Hitherto the radius has been described in *Moschops* by Broom (11) and Gregory (18). Of the radius of *Tapinocephalus* Broom (13) in 1928 says "the radius is broad and flat" and agrees with that of *Moschops* but is more massive. In 1929 Broom (14) described a radius of *Jonkeria* sp. and figured a right radius of "probably *Titanosuchus ferox*". In 1931 von Huene (21) gave a figure of a Deinocephalian radius. Byrne (16) figured the bone in *Moschoides* and I (4) figured the radius of a Moschopid in 1954.

Diag. 3.



A Titanosuchian radius and ulna in dorsal view. B.F.—flange for the insertion of the biceps; C.P.—coronoid process; in.—facet for intermedium; L.S.F.—lip to sigmoid fossa; R.—radius; ra.—facet for radiale; Sty.—styloid flange; U.—ulna; Ue.—facet for the ulnare.

In the larger Titanosuchians the radius is a large stout bone, but in some of the smaller forms it is relatively slender (length 190-318 mm.). The two ends are expanded, especially the proximal one in the larger forms. Both the ends and the shaft are oval in section. The proximal end is flat or

becomes convex towards the postaxial border, which abuts against the rim of the sigmoid facet of the ulna (but in *Keratocephalus* the whole proximal face is convex). On its postaxial corner there is a weak to strong flange (bicipital), whose edge fits into the hollowed surface of the ulna below the rim of the sigmoid facet. A similar flange is developed on the distal postaxial surface, where the radius fits against the ulna. The pre- and postaxial faces are deeply concave in the Titanosuchia, but the shaft is little constricted in *Keratocephalus* and some Moschopids. The preaxial edge is fairly sharp, whereas the postaxial edge is rounded. The distal end is fairly flat or quite strongly convex, and in some Titanosuchia shows a well developed facet for the intermedium and a lesser one for the radiale.

Ulna

In 1876 Owen (23) noticed as *Pareiasaurus* an ulna, which Seeley figured and, as Lydekker (22), considering it to be of *Tapinocephalus*, remarks "referred it in the abstract to *Titanosuchus*".' This is undoubtedly a Titanosuchian ulna notwithstanding that Broom (14) also considered it to be of *Tapinocephalus*. The supposedly *Titanosuchus* ulna figured by Seeley (28) is really a tibia of a Pareiasaurian. The *Moschops* ulna was figured by Broom (11) and refigured by Gregory (18), and in Broom's (10) photo of the "*Tapinocephalus*" fore-limb a large Titanosuchian ulna is shown. In 1914 Watson (29) mentioned the ulna of *Phocosaurus* and Broom (13) mentions an ulna of *Tapinocephalus* and figured (14) part of an ulna of *Jonkeria crassus* and describes the ulna of *Jonkeria* sp. In 1931 von Huene (21) figured an imperfect ulna of a Deinocephalian. Byrne (16) figured the bone of *Moschoides* and I (4) figured a Moschopid ulna in 1954.

In our collection there are 15 ulnae, some without the distal end. In no case is there a pair and in only two cases have we a radius associated with an ulna.

The Deinocephalian ulna is fairly to very massive and short (length 258-402 mm.). Its proximal end is greatly expanded; the shaft is broad but flattened; the postaxial face is fairly straight, but the preaxial face is deeply concave; the distal end is only slightly more expanded than the shaft. Proximally the lateral corner is developed into a strong olecranon which is rugosely striated for the reception of the strong triceps muscle. Medially lies the large sigmoid face for articulation with the humerus; this surface is only shallowly concave longitudinally and it is continued on to the strong coronoid process; dorsally to the coronoid process the sigmoid face ends, in its medial part, in a concave rim, to which the outer edge of the head of the radius is applied, so that the sigmoid face is continuous with the proximal face of the radius to form a conjoined articulatory facet for the capitellum

of the humerus. The sigmoid face has a more or less distinct ridge running proximo-distally so that two faces, inclined at an obtuse angle to each other, can be distinguished; the dorsal part articulates with the humerus when the limb is directed forwards, and the ventral part comes in play when the epipodium is rotated to the posterior position. The dorsal lip of the sigmoid face forms a more or less prominent rim, which is continued medially by the sharp edge of the head of the ulna. Lateral to this rim the dorsal surface of the ulna bears a longitudinal groove fading away distally on the shaft; on the ventral face there is a similar though deeper groove. The distal end is indistinctly divided into three facets; the central and larger facet is for the ulnare, the preaxial facet for the intermedium and the postaxial one for the weak pisiforme. Proximally of this facet for the pisiforme the postaxial edge of the ulna develops a sharp ridge, which apparently has the same function as a styloid process.

The Elbow Joint

For all major movements the two bones of the epipodial move as a unit and the articulatory face formed by the ulna and radius is in the shape of a fairly large arc whose surface moves over the distal end of the humerus in flexion and extension. When the radius is rotated on its long axis the ulnar facet slides backwards or forwards against the distal face of the humerus. Extension is limited by the olecranon, for which little provision is made in the form of a shallow trochlear fossa.

Manus

In the Deinocephalia the manus is insufficiently known. In the Moschopids the carpal formula is 3, 2, 5 Byrne (16) or 4, 1, 5 Boonstra (4) and the phalangeal formula 2, 3, 3, 3, 3 Byrne (16). In the Anteosauria I (4) recorded, in one specimen, a carpal formula 3, 1, 5 and the most unusual phalangeal formula 3, 3, 4, 4?, 2.

In the structure of the fore-limb the Deinocephalians show certain important advances beyond the Pelycosaur condition: in the humerus the proximal face has lost the elongated straplike articulatory face and the articulation is concentrated in a medially situated caput; the twist of the proximal and distal ends relative to each other is strongly reduced; the epicondyles are much reduced in size and there is never a separate supinator crest; the loss of the ectepicondylar foramen in all but the Titanosuchia; the distal position of the condyles makes a more upright disposition of the epipodial possible; the sigmoid face of the ulna forming a more widely open arc makes a greater

extension of the epipodial possible; the greatly laterally expanded delto-pectoral crest makes the area for the origin of the m. brachialis much greater.

C. *The Pelvic Girdle* (Diagram 4)

Owen (23), in 1876, was the first to examine elements of the pelvic girdle of a South African Deinocephalian. But, due to the confused labelling of the materials sent to the British Museum (N.H.), he mistakenly considered these to be Pareiasaurian, and also erroneously identified an ischium and pubis (B.M. 43525r) as parts of the pectoral girdle and humerus.

These pelvic elements were re-examined by Seeley (28) and made the type of a new genus, *Phocosaurus*. Lydekker (22) provisionally included this specimen in the genus *Tapinocephalus*, and Watson (29) refigured the pelvis.

In 1914 Broom (11) figured and described the pelvis of *Moschops*. This *Moschops*-material was re-examined by Gregory and Camp (17), Romer (25) and Gregory (18) and their restorations of the pelvis differ considerably from that of Broom.

Meanwhile Haughton (20) had published a photo of the mounted skeleton of *Struthiocephalus* showing the pelvis and on this Broom (15) based his reconstruction.

Broom (13) in 1928 figured an ilium and ischium under the name *Tapinocephalus atherstonei*, whereas they are in fact of a Titanosuchian.

In the following year Broom (14) described an ilium of *Jonkeria* sp. and another under the name *Dinosphageus haughtoni;* also an ischium under the name *Phoneosuchus angusticeps*. Both these have since been included in the genus *Jonkeria*.

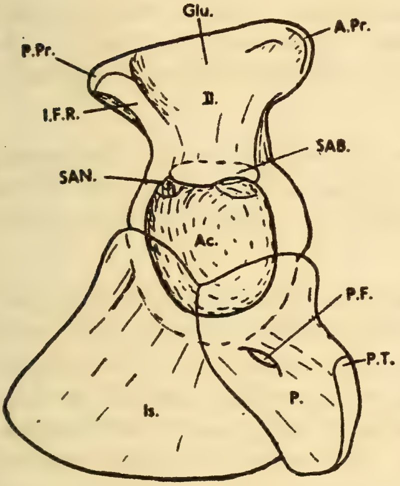
In 1931 von Huene (21) figured and described the ilium of *Keratocephalus* and Broili and Schröder (6) an incomplete ilium and pubis of *Titanognathus lotzi*, which has since been included in the genus *Anteosaurus*. Finally Byrne (16) gave a brief account of the imperfect pelvis of *Moschoides*.

In our collection the pelvic girdle is represented in 18 specimens. In only six cases parts of the pectoral girdle are associated with parts of the pelvic girdle of the same specimen.

The pelvis is much lower than the pectoral girdle and the antero-posterior length of the pubo-ischiadic plate is also less than that of the coracoidal plate.

The three bones of each half are mostly not firmly united at the sutures and in immature specimens the centre of the acetabulum may still be cartilaginous.

The two halves, meeting in the median line, are weakly united, and in immature specimens a large lacuna is present, which may persist as a small opening even in older specimens; but in life would be closed with cartilage.



The pelvis of a Titanosuchian in lateral view. Ac.—acetabulum; A.Pr.—anterior iliac process, more or less everted (lower in most Tapinocephalia); Glu.—area of origin of the ilio-femoralis (gluteus); I.F.R.—ilio-fibularis ridge (this lies more horizontally in most Tapinocephalia); Il.—ilium (lower in most Tapinocephalia); Is.—ischium (restored); P.—pubis; P.F.—pubic foramen; P.Pr.—posterior iliac process (lower and lying more horizontally in most Tapinocephalia); P.T.—tuberculum pubis; S.A.B.—supra-acetabular buttress; S.A.N.—supra-acetabular notch.

The junction of the pubes, particularly, is very weak, due to the eversion of the antero-ventral pubic edge. The ichial symphysis is stronger, but here the posterior median edges also diverge and no strong symphysial carina is developed.

The attachment to the vertebral column is by a pair of very stout main sacral ribs, assisted by three posterior ribs, which are very much weaker and decrease in functional importance in posterior direction, and by a long slender anterior lumbo-sacral rib usually with a feeble attachment to the everted anterior iliac process. The main sacral rib lies above and in the same plane as the acetabulum — it is thus not pre-acetabular but supra-acetabular.

The acetabulum is large and roughly circular in outline; all three bones help in its formation, with the iliac part constituting a half to two thirds. The acetabulum faces mainly outwards except in the Anteosauria where it is directed considerably ventrally. It is fairly shallow but with strong raised rims for the attachment of the joint capsule and ligaments. Dorsally a very strong buttress, stronger in the Titanosuchia than in the Tapinocephalia, overhangs the acetabulum (except in the Anteosauria), and this receives the main thrust of the femur. In its dorso-posterior corner, just posterior to the edge of the buttress, lies the large supra-acetabular notch.

The ilium is constricted above its acetabular part to form a neck or shaft; above this the blade is antero-posteriorly elongated, with a fairly long anterior iliac process and a shorter and weaker posterior process. In the Titanosuchia the supra-acetabular part of the ilium is high, whereas in the Tapinocephalia it is low to moderate. This also applies to both the posterior and the anterior

processes. The anterior process is everted, weakly in most Tapinocephalia and strongly in most Titanosuchia. The posterior process extends further posteriorly in the Tapinocephalia than in the Titanosuchia, and in the former lies more horizontally and in the latter more upright. On the posterior edge of the posterior process an everted or folded-over ridge is developed, presumably for the origin of the ilio-fibularis muscle. This ridge lies horizontally in nearly all the Tapinocephalia, where it forms a sharp to rounded postero-ventral edge, whereas it lies much vertically in the Titanosuchia, where it forms a rounded to swollen thickening anterior to the posterior edge of the ilium.

The upper iliac edge overhangs the area of origin of the m. ilio-femoralis (gluteus) in some Tapinocephalia. The gluteal area is shallow in the Tapinocephalia, but in some Titanosuchians it is deeply concave antero-posteriorly.

In dorsal view the outline of the upper iliac surface is roughly triangular. The apex, lying medially, is at a lower level than the outer iliac edge, which is fairly straight in the Tapinocephalia, but concave in the Titanosuchia. The apex represents a great thickening on the middle part of the inner surface of the ilium. The massive main sacral rib abuts against this thickening — more particularly to its anterior face. This sacral rib extends ventrally along the inner iliac face to a plane just dorsal to that in which the outer buttress lies. Posterior to the attachment of the main sacral rib there are three irregular depressions for the reception of the three weak posterior ribs, whose upper surfaces lie in the same plane as the upper surface of the main rib, but as they are weak the ventral extent of their contact with the ilium is small. On the inner face of the anterior iliac process there is an ill-defined area for the reception of the end of the lumbo-sacral rib. The inner face of the ilium, dorsal to the sacral ribs, afforded an area for the attachment of the axial muscles.

The ischium is only adequately known in the Tapinocephalia. Its antero-posterior length is fairly small. Except for its acetabular portion it is fairly lightly built. It forms the postero-ventral segment of the stout acetabular rim. From its junction with the ilium its postero-dorsal edge is thick but posteriorly rapidly decreases to a thin edge, without the development of an ischial tuberosity. Its ventral edge is curved so that posteriorly it is separated from its fellow by a triangular incisure. Similarly the anterior ends also do not meet, but here the opening between the ischia and pubes was closed by cartilage. The central part forms a fairly strong symphysial face. The ischia meet at an angle to form a V-shaped pelvic exit, and no carina is formed along the median line.

The pubis has its anterior corner strongly everted. From this corner to the acetabulum the upper border of the pubis is thickened to form a stout pubic ridge from which the pubo-tibialis muscle originated. The corner or the tuberculum pubis, for the insertion of Poupart's ligament, is strong. Below the pubic ridge there lies the oval pubic foramen. Owing to its eversion only the posterior part of the ventro-median pubic edge meets its fellow to form a very weak line of contact, and the antero-posterior length of the pubis is small. On the inner face it shows a quite distinct area from which the pubo-ischio-femoralis internus originated.

In the pelvis the Deinocephalia have advanced beyond the Pelycosaurian stage in that the pubo-ischiadic plate has been greatly reduced in length; the strong development of the anterior iliac process and the reduction of the posterior iliac process; in the development of a large circular acetabulum; and increased height and a greater width to the pelvic outlet.

It most obviously differs from the higher Therapsids in the retention of the simple pubic foramen and in the shortness of its pubo-ischiadic plate.

D. *The Hind-limb* (Diagrams 5 and 6)

The Femur

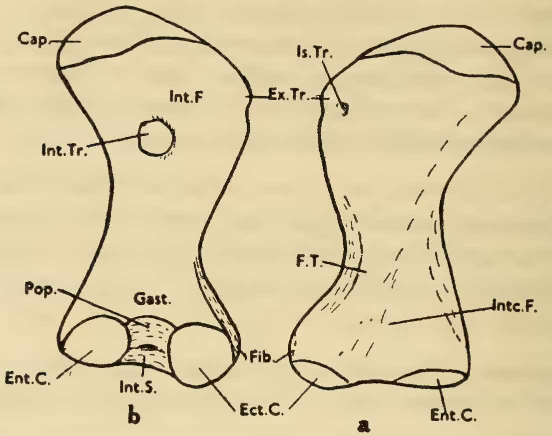
The first Deinocephalian femur from the Karroo to be described was a proximal half from Varsfontein (B.M. 43525t) first noticed by Owen (23) in 1876 under the name *Pareiasaurus bombidens* and figured by him (24) in 1880. Lydekker (22) referred this specimen to *Tapinocephalus*, and it will here be included in *Phocosaurus*.

Seeley (28) in 1889 figured (Pl. 19) a femur from Koedoeskop (B.M. 49368), which he considered to be associated, correctly I believe, with the type of Owen's *Titanosuchus ferox*. Broom (8) in his description of *Pelosuchus* mentions a femur, which he (15) figured in 1932. In 1914 Broom (11) figured a femur associated with the type material of *Moschops*, and figures of femora from this material were subsequently published by Gregory and Camp (17), Romer (25), Gregory (18) and Broom (15).

The femur of *Pnigalion* was figured by Watson (29) in 1914, and in the following year Broom (12) mentions that femora are associated with the type of jaws of *Moschognathus* and these were figured by Gregory (18). The femur of *Struthiocephalus* is shown in Haughton's (20) photo of the mounted skeleton. In 1928 Broom (13) figured a femur he thought to be of *Tapinocephalus*, but which in the sequel is shown to be of *Jonkeria*, and in the next publication (14) a femur of *Jonkeria* sp. In 1931 von Huene (21) figured the femur of *Keratocephalus* and Broili and Schröder (6) figured a distal end

of the Anteosaurian, *Titanognathus*. Byrne (16) gave figures of the femur of *Moschoides* and I (4) of *Micranteosaurus*.

Diag. 5.



The femur of a Titanosuchid. a. Dorsal view. b. Ventral view. Cap.—caput femoris; Ect.C.—ectocondyle; Ent.C.—entocondyle; Ex.Tr.—external trochanter; F.T.—origin of the femoro-tibialis; Fib.—facet for articulation of fibula; Gast.—origin of gastrocnemius; Intc.F.—shallow intercondylar fossa; Int.F.—intertrochanteric fossa; Int.S.—intercondylar sulcus; Int.Tr.—internal trochanter; Is.Tr.—insertion of ischio-trochantericus; Pop.—popliteal fossa.

In the collection of the South African Museum there are 37 femora of which some are only represented by one of the two ends. Although there are about an equal number of femora and humeri it is noteworthy that only in 8 specimens there are preserved both a humerus and a femur of the same individual.

The femur of the Anteosauria differs so markedly from that of the Tapinocephalia and the Titanosuchia that in this general account of the Deinocephalian femur it is not considered, but is treated of separately in the systematic part of this paper.

The femur, always longer than the humerus, is a massive bone with very little of a shaft but with expanded ends. The proximal end is always wider than the distal end. There is a very little "twist" on the shaft so that the two ends lie in nearly the same plane, but the distal pre-axial condyle does lie a little more ventrally than the distal post-axial condyle. The post-axial condyle also lies a little further distally (where it lies much distally this appears to be due to postmortem deformation or is pathological). The shaft is always much broader than thick. In dorsal view the pre-axial border is more concave than the post-axial border. In pre-axial view the ventral border is more concave than the dorsal and the long axis is straight.

Proximally the caput femoris is terminal, but somewhat preaxially directed; it is antero-posteriorly elongated, thick preaxially, where it has an abrupt edge; but postaxially it tapers more or less gently towards the external trochanter from which it is sometimes separated by a slight notch; in its preaxial part the caput is moderately convex. The caput is much smaller than the acetabulum — its dorso-ventral diameter being about a third to a quarter of that of the acetabulum.

The external trochanter lies far postaxially to form the proximo-postaxial corner of the femur; from here the postaxial edge of the bone sweeps inwards with a fairly straight edge to the shaft and then more or less sharply outwards again to form the outer border of the ectocondyle. On the dorsal surface just preaxial to the external trochanter some femora have a slight pit, where the ischio-trochantericus muscle was presumably inserted.

The internal trochanter (sometimes not evident) is a rounded or oval tubercle, sometimes very prominent, lying on the ventral surface, well away from the preaxial border so that the intertrochanteric fossa lies well postaxially.

The distal articulatory facets for the tibia lie far distally and face only little ventrally; the outer facet is slightly larger than the inner and lies a little further distally. The two facets are separated by a deep and wide intercondylar sulcus, which proximally has a sharp ridge separating it from the popliteal fossa, and distally passes over into a shallow intercondylar notch; a rounded depression in the proximal part of the intercondylar sulcus presumably housed the quadriceps tendon.

The dorsal surface of the femur shows few prominent features; the intercondylar fossa is very shallow; from the outer condyle an oblique ridge runs in the direction of the caput femoris; between this ridge and the external trochanter the ilio-femoralis muscle has a large area of insertion; the femoro-tibialis originated from the middle part of this ridge.

On the postaxial face of the ectocondyle lies the weakly modelled surface to which the bipartite head of the fibula articulated.

The Deinocephalian femur has advanced beyond the Pelycosaur stage by the breaking up of the Y system of ridges; lack of a 4th trochanter; decreased "twist" on the shaft; the distal position of the condylar facets, but with the ectocondyle nearly in the same plane as the entocondyle and with a larger articulatory face. The widening of the whole bone and the flattening of the shaft is apparently a secondary approach to the Pareiasaur condition. It differs from the higher Therapsids in the great width and the lack of a long distinct shaft and the caput is not turned antero-dorsally.

The Hip-joint

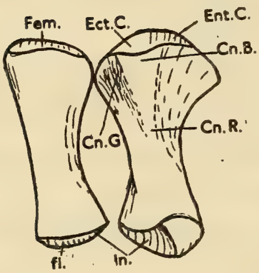
The Deinocephalian hip-joint is a very ill-fitting joint. The elongated caput femoris requires for its rotation on its long axis the very large circular

acetabulum in which it fits very insecurely so that the strong iliac buttress is required to prevent its dislocation when the thrust is transmitted. The femur in transmitting the thrust would lie obliquely with its distal end considerably lower than the caput and it would have great, but not very secure, possibility for antero-posterior movement. A very strong capsule and ligaments would be required to strengthen the joint.

The Tibia

Owen (23) mentions a tibia (B.M. R.1707) referred by him to *Pareiasaurus bombidens*. This tibia was figured by Seeley (28) who said "it may be new or it may be *Pareiasaurus* or *Tapinocephalus*". Considered by Lydekker (22) as *Tapinocephalus*, it probably really is *Titanosuchus*. Two other tibiae (one 47100) are mentioned by Lydekker as probably *Titanosuchus* or allied form.

Diag. 6.



A Titanosuchid tibia and fibula in dorsal view. Cn.B.—cnemial boss; Cn.G.—cnemial groove; Cn.R.—cnemial ridge; Ect.C.—facet for the outer femoral condyle; Ent.C.—facet for the inner femoral condyle; Fem.—proximal facet on fibula for articulation with outer surface of the ectocondyle; fi.—facet for the fibulare; in.—facet for the intermedium.

The tibia of *Moschops* was figured by Broom (11) and refigured by Gregory (18). In 1914 Watson (29) mentions a tibia as part of the type material of *Phocosaurus* and stated that the tibia of *Titanosuchus* "does not differ essentially from that of the Tapinocephaloids". In Haughton's photograph (20) a tibia of *Struthiocephalus* can be seen.

In 1928 Broom (13) figured a tibia, which I believe to be Jonkeri, as that of *Tapinocephalus atherstonei*, and, in the following year, he (14) figured the tibia of *Jonkeria truculenta* and noticed that of *Jonkeria* sp. In 1931 von Huene (21) figured the tibia of *Keratocephalus* and Byrne (16) in 1940 that of *Moschoides*.

In the collection of the South African Museum the tibia is represented by 17 more or less complete bones. It is remarkable that so many more tibiae than radii should be preserved. Only in one case both right and left tibia of the same animal are present. In seven cases we have a tibia with a fibula in the same specimen.

The tibia is in size medium to large and fairly to very massive with strongly expanded ends and a robust shaft. The length varies from 180-355 mm. On its dorsal surface there is a very strong cnemial protuberance for the insertion of the tendon of the femoro-tibialis and associated muscles. This boss extends distally as a rounded ridge, which fades out on the shaft before reaching the middle of the bone. Postaxially of the cnemial ridge lies a fairly shallow groove bounded further postaxially by a weak ridge lying parallel to, but is much weaker than the cnemial ridge. The proximal expansion flares out preaxially as does also the distal expansion so that the preaxial border is deeply concave. The proximal expansion flares out less postaxially, but the distal expansion flares out abruptly postaxially.

The proximal surface is essentially triangular in outline with the apex formed by the massive cnemial boss. Above the cnemial eminence the surface is convex, but this flattens out towards the ventral corners, with the formation of a low indistinct ridge separating these two flattened faces. The preaxial face is greater than the postaxial one and they correspond to the two condylar faces of the femur. In a tibia of *Struthiocephalellus* a high ridge separates two concave faces.

The distal surface is strongly convex for the two-thirds of the surface lying preaxially; the postaxial part is flattened and tends to be concave.

The ventral surface is separated from the postaxial face by a strong ridge and is furthermore indistinctly divided into two parts by a ridge running obliquely, with its distal end lying preaxially; the upper part receives the long ventral muscles and the lower the short ventral muscles.

The Fibula

The fibula has hitherto been described by Seeley (28) in *Titanosuchus* and this identification is probably correct, although Broom (14) does not think the bone is a fibula at all; in *Moschops* by Broom (11) and refigured by Gregory (18); seen in Haughton's (20) photograph of *Struthiocephalus; in errore* by Broom (13) for *Tapinocephalus* and (14) in *Jonkeria truculenta* and *Jonkeria* sp. and finally by Byrne (16) in *Moschoides*.

In the collection described here there are 16 fibulae, of which only a couple are not very well preserved.

Although the weakest of the major limb-bones the Deinocephalian fibula is still a stout bone (length 220-345 mm.). The proximal expansion is great and moderately to very massive; the distal end is somewhat less expanded, but still quite strong; the postaxial edge is rounded and is in outline fairly straight, whereas the preaxial border is deeply concave and this edge is sharp up to near the distal end where it becomes rounded, with a sharp ridge lying more ventrally; the shaft is long, fairly wide but

flattened, and there is very little "twist" on the shaft, but the distal end is bent down preaxially so that the two ends do not lie in the same plane.

The proximal facet is convex in section and occupies the whole of the proximal end; although terminal it faces ventrally; in outline it is reniform with the hilus due to a hollowing out of the ventral edge; a thickening on the medio-dorsal surface near the head was for the insertion of the ilio-fibularis muscle.

The distal facet is broad but flattened, convex, thicker preaxially and facing more preaxially; the tilted preaxial part articulating with the intermedium and the postaxial part with the fibulare.

The Knee Joint

The thrust of the hind foot is along the long axis of the tibia and is transmitted to the two femoral facets meeting the proximal end of the tibia in an efficient joint. As the articulatory surfaces on the femur lie much distally and curve round dorsally the lower leg can be greatly extended to bring the long axes of the tibia and femur nearly in line. Rotation of the tibia on its long axis is well allowed for with the fibula sliding over the postaxial corner of the femur and distally carrying the foot with it. In the Titanosuchia the amount of the extension possible is thus much greater in the hind-epipodial than in the fore-epipodial.

The Pes

The Deinocephalian pes is but poorly known; in the Titanosuchia the proximal row of tarsals consists of an intermedium and fibulare; in the Moschopids (16) the tarsal formula is 2, 1, 4 and the phalangeal formula apparently 2, 3, 3, 3, 3; in a single Anteosaurian I (4) recorded a tarsal formula 2, 1, 5 and a phalangeal formula 2?, 3?, 3?, 4?, 2.

Systematic Descriptions

Deinocephalia

Sub-ordinal Characters of the Girdles and Limbs.

The pectoral girdle is structurally Therapsid, but comparatively large and massive and without an acromion; the cleithrum is splintlike or well developed; the interclavicle with its anterior spatulate end turned upwards; the three scapulo-coracoid elements not firmly ankylosed; there is no ossified sternum.

The humerus is structurally Therapsid but comparatively massive and with either one or two epicondylar foramina; the radial facet is either much distally or much ventrally situated.

The ulna has a massive olecranon.

The pelvic girdle is structurally Therapsid but large and massive; the pubo-ischiadic plate is short; the acetabulum large; there is only a simple pubic foramen; in most groups there is developed a distinctive ridge on the posterior edge of the posterior iliac process for the origin of the m. ilio-fibularis; the anterior pubic edge is everted; the symphisis is weak.

The femur, of typically Therapsid structure, is either short and massive or long and slender.

Tapinocephalia

Infra-ordinal Characters of the Girdles and Limbs.

The pectoral girdle is fairly light to moderately massive; the scapula is fairly low to low (310-530 mm.) with the upper part of its blade fairly narrow to fairly broad (120-270 mm.); the scapular head of the triceps originates from a low mound; the internal opening of the foramen supra-coracoideus does not open into or is connected by a groove to the subscapular groove; the glenoidal facet of the scapula is small or of medium size and faces little or not at all externally.

The coracoidal plate is fairly short or long antero-posteriorly; the pre-coracoid is fairly large, but fairly weak with a thin anterior border and a fairly strong dorso-posterior apex; the precoracoid excluded from the glenoid or just enters the rim; its outer face is only moderately convex.

The coracoid is small to medium, light to fairly strong with a fairly large glenoidal facet facing dorso-posteriorly and also much externally. Except near the glenoid the three bones of the scapulo-coracoid are weakly united suturally.

The clavicle is a medium-sized flattened bone with expanded ends and a slight waist.

The cleithrum is a weak splintlike bone.

The interclavicle is a moderately light bone, moderately expanded anteriorly with a long slender to fairly slender stem. A shallow groove receives the lower end of the clavicle.

The humerus is fairly light to moderately massive; it varies in size from small to large (length 276-588 mm.), but is never short and squat, and some-times long and fairly slender; there is never an ectepicondylar foramen; the capitellum is weak to moderately strong and usually poorly modelled and it never extends proximally along the ventral face but remains situated

much distally; the processus medialis always lies far proximally, nearly in the same plane as the caput; the processus lateralis always lies far proximally; the proximal expansion is moderately great to great; the epicondyles are moderately to greatly expanded; the shaft is short to long, narrow to very broad; the ventral opening of the entepicondylar foramen is always slitlike.

The ulna is small and light to moderate and fairly strong, or is short, massive and squat.

The radius is long and slender or fairly short with strongly expanded ends.

In the manus the carpal formula is 4, 1-2, 5, and the phalangeal formula is 2, 3, 3, 3, 3.

The pelvis has a fairly long pubo-ischiadic plate; the iliac blade is low to only moderately high; the ilio-fibularis ridge has a fairly sharp edge and is only moderately strong and usually lies nearly horizontally; the anterior iliac process is only slightly to moderately everted; the posterior iliac process is fairly long and low; the outer iliac face is only slightly concave in antero-posterior direction.

The femur varies from fairly small to fairly large (length 276-468 mm.), light, moderate to fairly robust, sometimes short and squat; the internal trochanter undeveloped or forming and elongated tubercle situated well away from the preaxial border; the width over the external trochanter is small (95 mm.) to great (256 mm.), and without a notch.

The tibia is massive and short (232 mm. in length) or slender or moderate (length 180-270 mm.).

The fibula is light and slender (length 222-288 mm.).

In the pes the tarsal formula is 2, 1, 4, and the phalangeal formula 2, 3, 3, 3, 3.

Tapinocephalidae

Family Characters of the Girdles and Limbs.

The pectoral girdle is only moderately massive; the scapula is low, with its posterior edge fairly straight.

The humerus is fairly massive but fairly long.

The ulna is moderate and fairly long or it is massive and squat.

The iliac blade is low with both the anterior and posterior processes long and low; the ilio-fibularis ridge is strong and prominent.

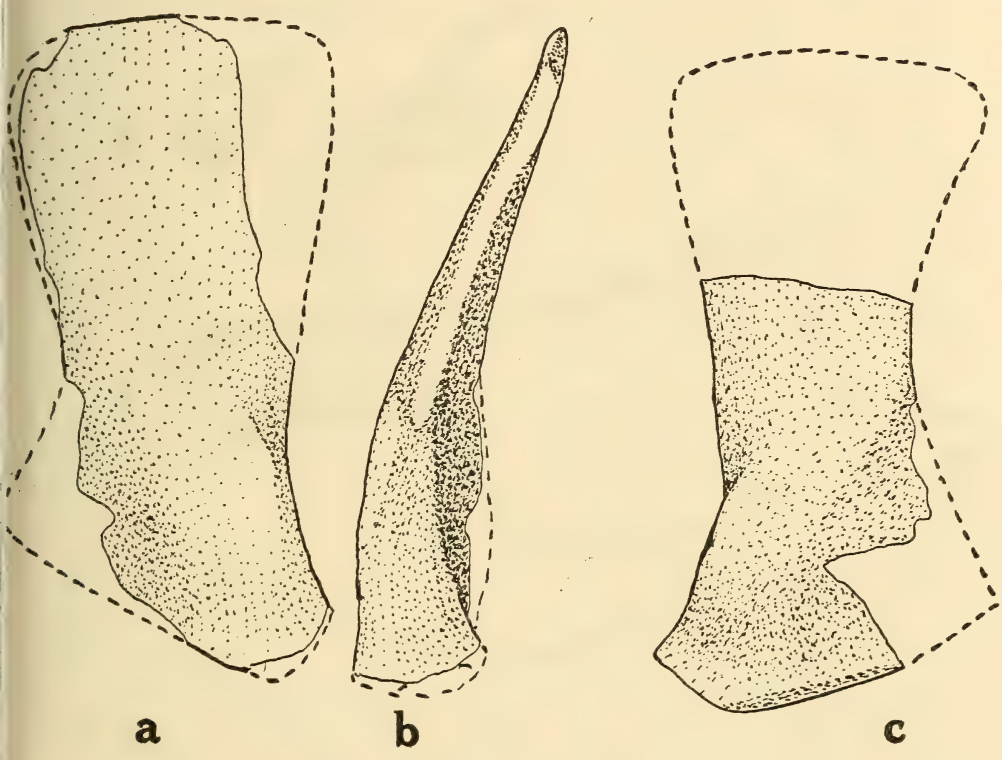
The femur is either fairly massive and fairly long or massive and squat.

The above statement on the characters of the girdles and limbs of the Tapinocephalidae is based on very inadequate material, as will become evident below.

Genus *Tapinocephalus* Owen (Figs. 1 a-b and 2)

In the collection of the South African Museum there is only one specimen in which there is an identifiable skull associated with some parts of the postcranial skeleton. This skull (S.A.M. 2344) is associated with two humeri and a scapula (S.A.M. 3355).

Fig. 1.

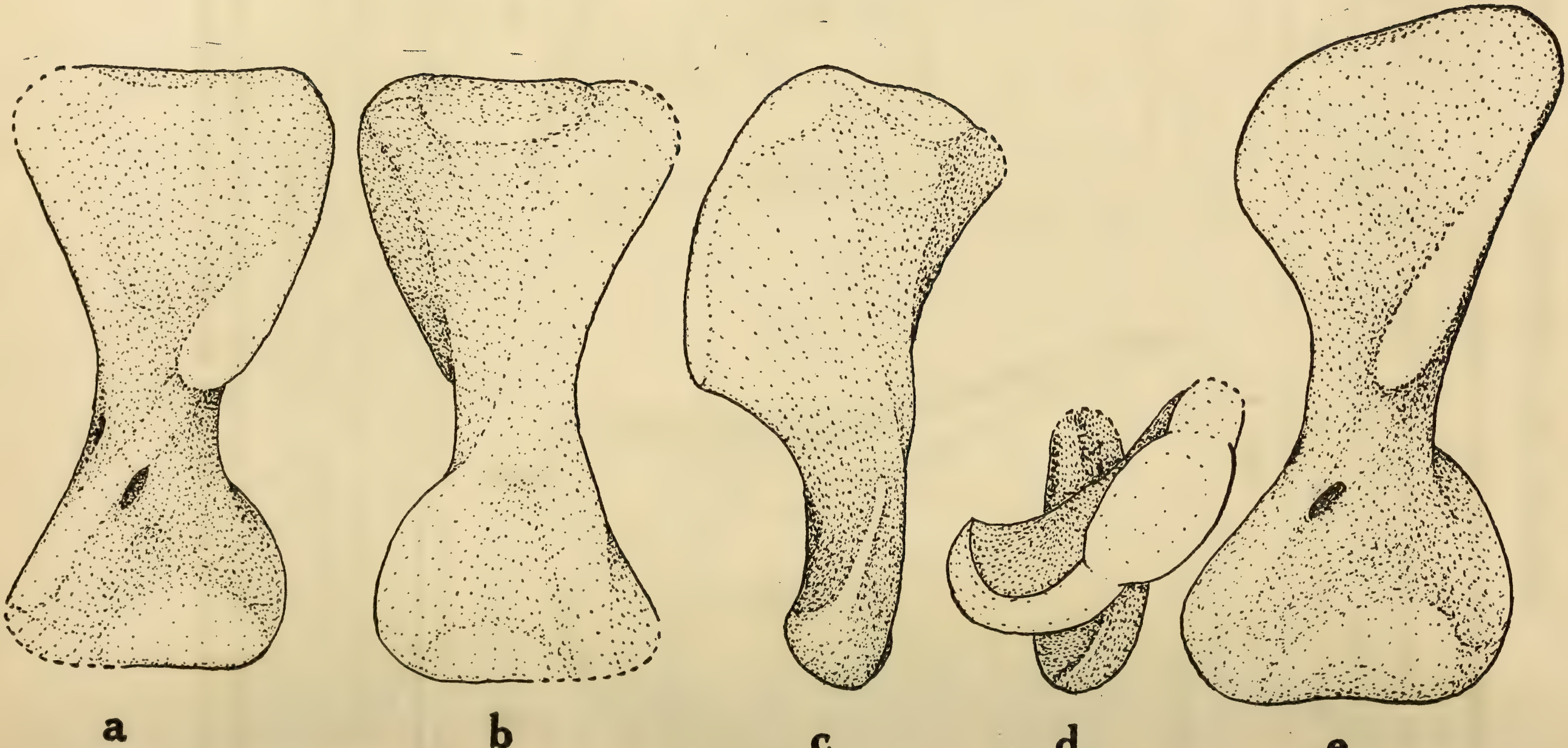


Scapulae. a. *Tapinocephalus atherstonei,* S.A.M. 3355. Lateral view. (× ⅛.) b. *Tapinocephalus atherstonei,* S.A.M. 3355. Posterior view. (× ⅛.) c. *Keratocephalus moloch,* S.A.M. 11937. Lateral view. (× ⅛.)

Note: All the figures in this paper are orthoprojections and not perspective drawings. In the girdles the figures labelled "lateral view" are of the bones in natural position projected on to the median plane, "anterior" and "posterior" are on to the one plane at right angles to the median plane and "dorsal" and "ventral" on to the other plane at right angles to the median plane.

The scapula (Fig. 1 a-b) is relatively low (530 mm.), with a broad blade (as reconstructed the width in its upper part is 270 mm.); the tricipital

Fig. 2.



Humeri of *Tapinocephalus atherstonei*. (× $\frac{1}{6}$.) a. S.A.M. 3355. Ventral view. b. S.A.M. 3355. Dorsal view. c. S.A.M. 3355. Anterior view. d. S.A.M. 3355. Proximal view. e. S.A.M. 5007. Ventral view. Note: In the humeri "ventral" and "dorsal" are projections on to the plane of the dorsal surface of the epicondyles, "anterior" is on to the axial plane at right angles to the above and "proximal" on the other plane at right angles to the first two.

ridge forms a strong but low mound; the internal opening of the foramen supracoracoideus does not open into the subscapular groove, which is very shallow indeed; the glenoidal facet is small and faces postero-ventrally and but very little externally; the upper part of the blade is fairly straight with little curvature to fit round the thorax.

The humerus (Fig. 2). Associated with the skull from Uitkyk (S.A.M. 2344), described by Haughton and correctly referred to *Tapinocephalus*, there is a fairly complete left humerus and a weathered proximal half of the right humerus (S.A.M. 3355). This association enables us to clear up the confusion which exists in regard to the *Tapinocephalus* humerus. The story of this confusion is as follows: In the first instance Owen (23) mistakenly referred the humerus B.M. 43525p from Varsfontein, Prince Albert, to *Pareiasaurus*. Lydekker (22), in correcting this obviously mistaken identification, himself erroneously referred it to *Tapinocephalus*. Broom (12), accepting Lydekker's identification, subsequently referred a specimen which he sold to the American Museum (A.M.N.H. 5611) to *Tapinocephalus*. Later Broom (13) figured a humerus (collection not stated) and states that this represents the true humerus of *Tapinocephalus* and at the same time refers B.M. 43525 to *Titanosuchus*. To make the confusion more confounded Broom then contradicts Seeley's (28) identification of B.M. 49369 as the humerus of *Titanosuchus* and refers this humerus to *Tapinocephalus*.

The Uitkyk humerus (S.A.M. 3355) associated with a *Tapinocephalus* skull, has no ectepicondylar foramen. In this feature it agrees with the known humeri of all the other members of the infra-order Tapinocephalia. Whereas all the humeri known to be associated with skulls classified as belonging to the infra-order Titanosuchia do have a well-developed ectepicondylar foramen. Thus quite apart from other features still to be considered below, the humeri A.M.N.H. 5611, B.M. 49369 and Broom 1928 (no collection or number given) must all belong to some genus of the Titanosuchia. B.M. 49369 should be left where Seeley put it, viz. in the genus *Titanosuchus* and A.M.N.H. 5611 in *Jonkeria* and Broom's 1928 humerus in *Scapanodon* and B.M. 43525 is the humerus of *Phocosaurus*.

The humerus of *Tapinocephalus* may be described as follows: very large (length 520-590 mm.); not very massive; proximal expansion great (width 276 mm.); distal expansion moderate (width 246-282 mm.); shaft fairly long and moderately thick (diams. 105 × 90 mm.); the delto-pectoral crest long, strong, terminating well proximal of the ventral opening of the entepicondylar foramen; caput oval in outline and lying in the same plane as the processus medialis and the processus lateralis; the processus medialis thus lies far proximally; the capitellum (radial condyle) is not well modelled, is weak, and lies much distally with its ventral part lying well distal of the plane in which the entepicondylar foramen opens; twist on shaft fairly

great (35°—40°); the lateral median line is weak and the antero-dorsal ventral line is fairly weak; the entepicondyle is not greatly expanded and the foramen enters ventro-postaxially and leaves in a narrow ventral slit; the ectepicondyle is moderately expanded to form a thin unperforated curved plate with a sharp edge.

No other bones of the girdles or limbs in *Tapinocephalus* are known with any certainty, but below it will be seen that certain elements could probably be those of *Tapinocephalus*.

Tapinocephalus atherstonei Owen

The specific description is as for the genus.

Referred specimens in the S.A.M. collection:

S.A.M. 3355. An imperfect left scapula (Fig. 1 a-b), a good left humerus (Fig. 2 a-d) and the weathered proximal end of the right humerus, associated with a good skull. Uitkyk, Beaufort West. Low *Tapinocephalus* zone. Coll. Haughton.

S.A.M. 5007. An isolated good left humerus (Fig. 2e). Wilgerfontein, Prince Albert. Low *Tapinocephalus* zone. Coll. Haughton.

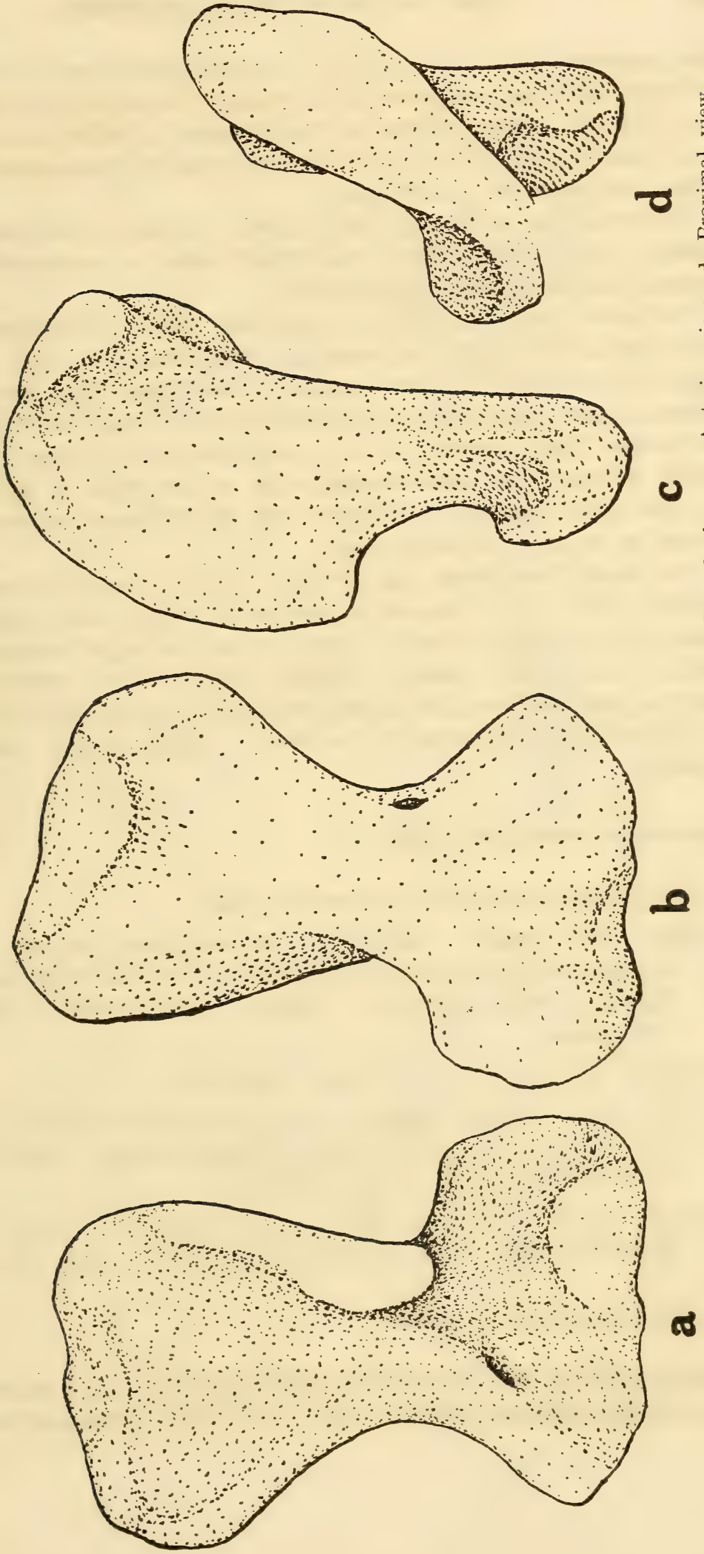
Genus *Phocosaurus* Seeley

This description is based mainly on the Varsfontein material in the British Museum (B.M. 43525), incorporating the accounts of Seeley (27), Lydekker (22) and Watson (29).

The pectoral girdle is large and massive; the scapula probably fairly low (lower than reconstructed by Watson, Fig. 11, which is given $\times \frac{1}{3}$, whereas it is in fact $\times \frac{1}{6}$); the scapular blade is fairly broad (240 mm.); the tricipital ridge is low; the glenoidal facet faces well externally. The precoracoid is inadequately known; "foramen opens into a distinct pit on the visceral surface" (Watson). The coracoid is massive with the facet facing much externally.

The humerus (Fig. 3) is large and massive (length 492 mm.); proximal (276 mm.) and distal (306 mm.) expansions large; shaft short and wide (diams. 168 $\times$ 96 mm.); the delto-pectoral crest very long and nearly reaching the plane of the ventral opening of the entepicondylar foramen; the caput is widely oval and lies in the same plane as the processus medialis and the processus lateralis, which also lies far proximally; the radial condyle is strong, fairly thick and well modelled, but situated much distally and not extending much proximally along the ventral face and thus well distal of the plane in which the entepicondylar foramen opens; the twist on the

Fig. 3.



Humerus of *Phocosaurus megischion.* ($\times \frac{1}{6}$.) B.M. 43525. a. Ventral view. b. Dorsal view. c. Anterior view. d. Proximal view.

shaft moderate (25°); the L.M.L. is fairly distinct and the A.D.V.L. is not prominent; the entepicondyle is strongly developed as a thick plate of bone and the ventral opening of the foramen is slitlike and situated well away from the edge of the bone; the ectepicondyle is developed as a greatly flaring thin sheet of curved bone

The ulna (see Seeley's Pl. 22) is short (320 mm.); the dorsal lip to the sigmoid face is fairly strong; the styloid ridge is prominent; width over coronoid process is moderate (204 mm.).

The pelvis (see Seeley, Pl. 21, Lydekker, Fig. 17 and Watson, Fig. 13). The pubo-ischiadic plate is short (as reconstructed ± 80% of the total height of the pelvis); the ilium appears to have been fairly low in its supra-acetabular part and fairly long antero-posteriorly; the ilio-fibularis ridge on the posterior iliac process lies fairly horizontally and appears to have been thickly rounded; the antero-ventral edge of the pubis is strongly everted with the tuberculum pubis confluent with the thickened antero-ventral edge curving in towards the median line.

The femur (see Owen (24), Pl. 17, Fig. 8) is only represented by a proximal half. The proximal expansion is fairly broad (225 mm.); the preaxial face is fairly deeply concave with the caput directed well pre-axially; caput fairly massive; external trochanter not distinctly separated from the proximal face; the internal trochanter lies well in and is developed as a prominent oval tubercle; the shaft is fairly slender (diams. 112 × 72 mm.).

Phocosaurus megischion Seeley

The specific description is as for the genus.

Type: B.M. 43525. Incomplete coraco-scapulae, humeri, right ulna, incomplete pelvis and the proximal half of the right femur. Varsfontein, Prince Albert. Middle *Tapinocephalus* zone. Coll. Atherstone.

Referred specimens in the S.A.M. collection:

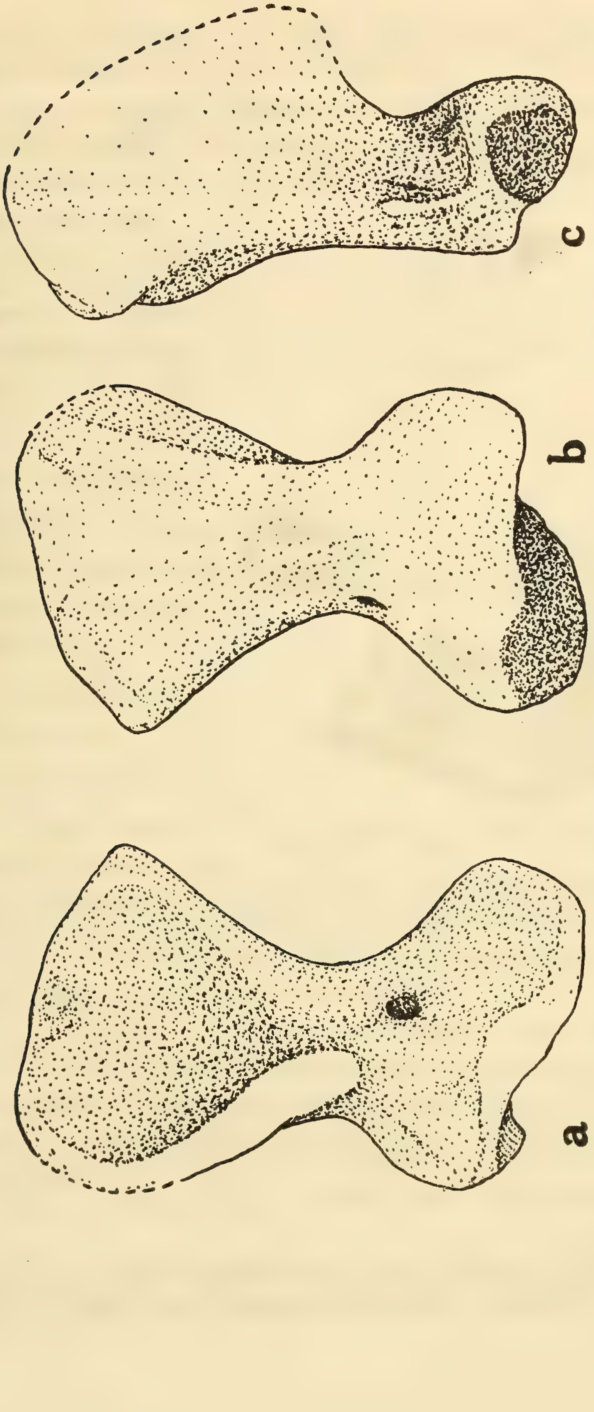
S.A.M. 11300. (Figs. 4 and 5.) A right humerus, showing a pathological lesion and an incomplete ilium. Deesweesfontein, Laingsburg. Low *Tapinocephalus* zone. Coll. Boonstra.

S.A.M. 11988. Proximal half of an isolated left femur. Boeteka. Beaufort West. High *Tapinocephalus* zone. Coll. Boonstra.

Genus *Keratocephalus* v. Huene

Although there are four skulls of *Keratocephalus* in the collection of the South African Museum there are only a few bones of the girdles and limbs,

Fig. 4.



Humerus of *Phocosaurus megischion.* ($\times \frac{1}{6}$.) S.A.M. 11300. (Distal end showing erosion resulting from a pathological lesion.) a. Ventral view. b. Dorsal view. c. Anterior view.

but, together with von Huene's account of some bones in Tübingen, the following incomplete description can be given.

Of the pectoral girdle only a piece of a scapula (Fig. 1c) is known and this is very similar to the corresponding part of the scapula of *Tapinocephalus*.

In the collection there are two imperfect ulnae (Fig. 6a). The ulna is massive and squat (length ± 350 mm.); the styloid ridge is prominent; broad over the shaft and very broad over the coronoid process.

Fig. 5.

Ilium of *Phocosaurus megischion*. (× 1/6.) S.A.M. 11300. Lateral view.

The only known radius (Fig. 6 b-d) is massive and squat (length 240 mm.); the ventral face is concave with a strong longitudinal ridge; the flange (for the insertion of the biceps) on the proximo-postaxial corner is strong; the proximal facet is convex.

With no pelvis in this collection I am extracting the characteristic features from von Huene's (21) account.

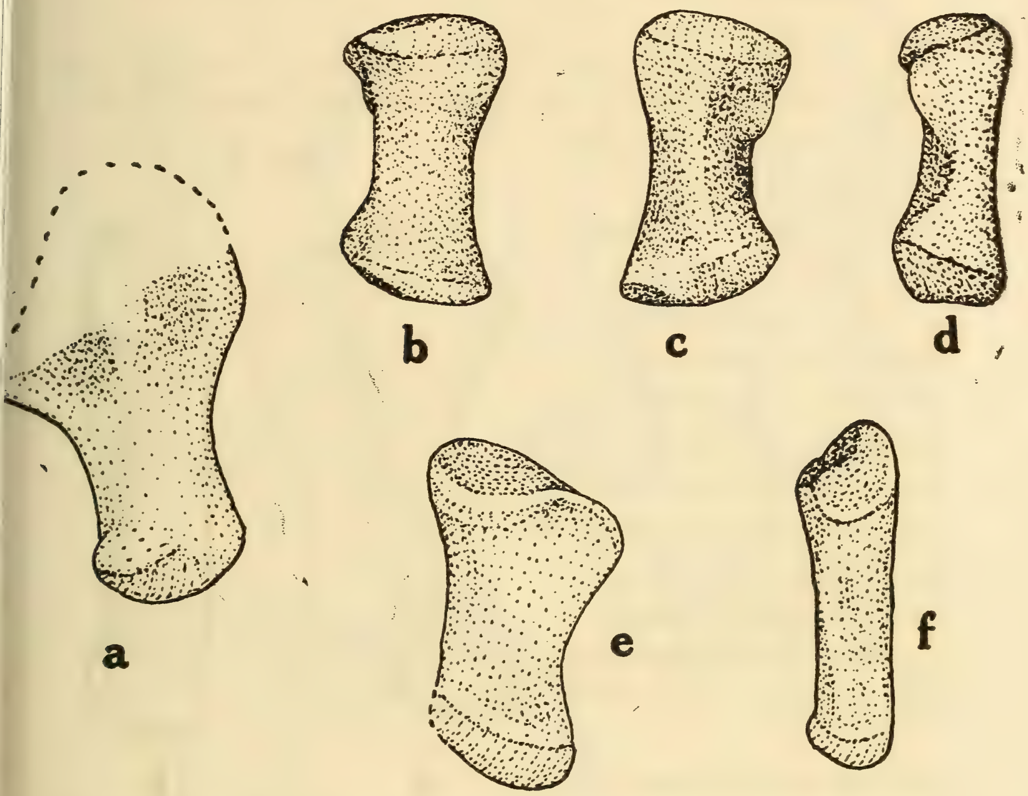
The supra-acetabular part of the ilium is low and very long (the height is only 52% of its antero-posterior length); the anterior process of the iliac blade is very long and low and is fairly strongly everted; the low posterior process is fairly long, but much shorter than the anterior process, with the ilio-fibularis ridge sharp and prominent and lying horizontally; the dorsal iliac edge is not folded over laterally; on the inner face of the anterior process there is a large face to receive a rib lying anterior to the main sacral rib.

The femur (see v. Huene's Figs.) is short (400 mm.) and broad; the width over the external trochanter is 256 mm.; the preaxial face is deeply concave with the caput much preaxially directed; the external trochanter is not demarcated from the proximal face, which extends far outwards from the caput; the internal trochanter developed as a prominent tubercle; the shaft is short and wide (diams. 132 × 84 mm.); the distal facets are terminal.

With only one crushed tibia in our collection (Fig. 6 e-f) and the one figured by von Huene, the *Keratocephalus* tibia appears to be massive

but short (length 232-276 mm.) with a broad shaft and a massive cnemial eminence.

Fig. 6.



Keratocephalus moloch. (× ⅛.) a. Ulna of S.A.M. 11937. Dorsal view. b. Radius of S.A.M. 11937. Dorsal view. c. Radius of S.A.M. 11937. Ventral view. d. Radius of S.A.M. 11937 Posterior view. e. Tibia of S.A.M. 8946. Dorsal view. f. Tibia of S.A.M. 8946. Posterior view.

Keratocephalus moloch von Huene

The specific description is as for the genus.

Type: Tübingen. An ilium, femur and tibia, associated with parts of the skull. Abrahamskraal, Prince Albert. Low *Tapinocephalus* zone. Coll. v. Huene.

Referred specimens in the S.A.M. collection:

S.A.M. 8946. An imperfect left ulna and a crushed left tibia (Fig. 6 e-f), associated with a skull. Mynhardtskraal, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

S.A.M. 11937. An imperfect right scapula (Fig. 1c), an imperfect left ulna (Fig. 6a) and a good right radius (Fig. 6 b-d), associated with a skull. Buffelsvlei, Beaufort West. Low *Tapincephalus* zone. Coll. Boonstra and Marais.

Genus *Pelosuchus* Broom

A part of the scapula preserved indicates a fairly close similarity to the scapula of *Keratocephalus,* as does also the incomplete weathered coracoid.

The femur (Fig. 7) is fairly short (420 mm.) and broad; the width over the external trochanter is 215 mm.; the preaxial face is deeply concave with the caput directed much preaxially; the external trochanter does not appear to be demarcated by a notch from the proximal face; the internal trochanter lies near the middle of the bone far away from the preaxial border and is a prominent and strong tubercle; the shaft is fairly strong and broad (diams. 132 × 80 mm.); the distal facets are terminal.

A distorted tibia appears to be stout and short with a strong cnemial eminence.

Fig. 7.

Femur of *Pelosuchus priscus.* (× 1/8.) S.A.M. 918. a. Ventral view. b. Anterior view. Note: In the femur "dorsal" and "ventral" are projections on the plane in which the ventral faces of the condyles lie and "anterior" on to the axial plane at right angles to the above.

Pelosuchus priscus Broom

The specific description is as for the genus.

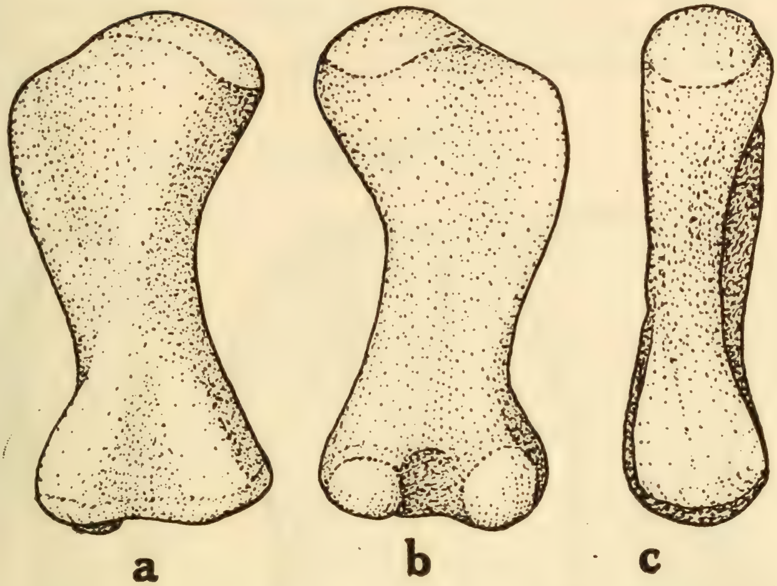
Type: S.A.M. 918. Part of a scapula, coracoid, a fairly good femur (Fig. 7) and distorted tibia, associated with a weathered dentary. Bokfontein, Prince Albert. Middle? *Tapinocephalus* zone. Coll. Cairncross.

Generically Undetermined Specimens:

S.A.M. 2753. A middle portion of a humerus (Fig. 12a) and the distal end of a femur. Viviers Siding, Beaufort West. Mid *Tapinocephalus* zone. Coll. Haughton and Whaits.

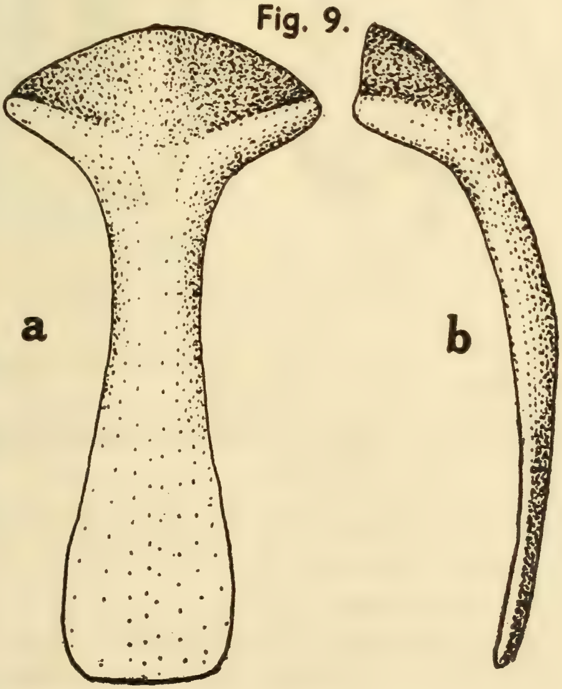
S.A.M. 9097. An isolated femur (Fig. 8). This is probably a femur of *Tapinocephalus*. Merweville Commonage. Low *Tapinocephalus* zone. Coll. Boonstra.

Fig. 8.



Above: Femur, probably of *Tapinocephalus*. ($\times \frac{1}{8}$.) S.A.M. 9097. a. Dorsal view. b. Ventral view. c. Anterior view.

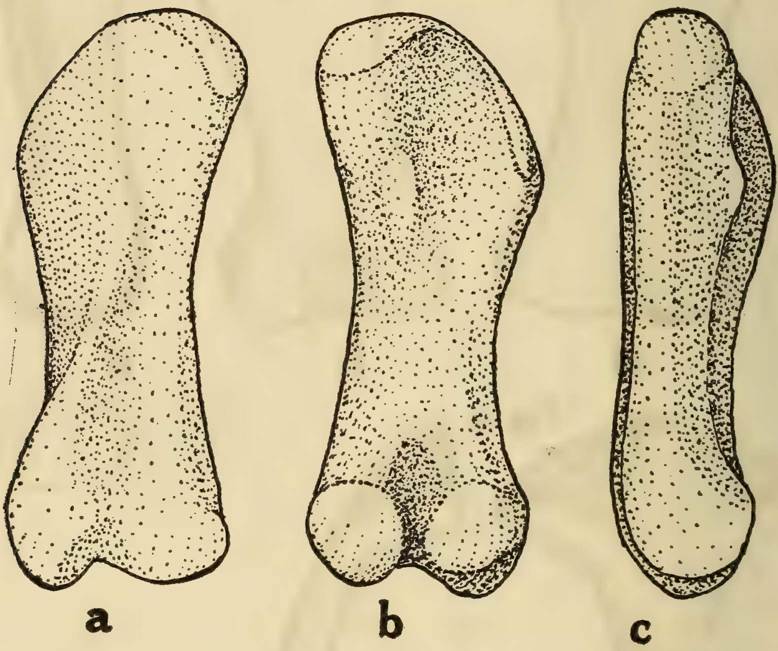
Fig. 9.



Left: Interclavicle of ? *Tapinocephalus*. ($\times \frac{1}{8}$.) S.A.M. 9153. a. Ventral view. b. Lateral view.

S.A.M. 9153. An interclavicula (Fig. 9) and a distorted femur (Fig. 10). The interclavicle has a long slender stem and the femur a ridgelike internal trochanter. These may represent a genus lying between *Tapinocephalus* and *Struthiocephalus*. Jacobskraal, Prince Albert. Low *Tapinocephalus* zone. Coll. Boonstra.

Fig. 10.



Femur of ? *Tapinocephalus*. ($\times \frac{1}{6}$.) S.A.M. 9153. (Slightly distorted.) a. Dorsal view. b. Ventral view. c. Anterior view.

S.A.M. 9164. The middle portion of a humerus. Wakkerstroom, Prince Albert. Low *Tapinocephalus* zone. Coll. Boonstra.

S.A.M. 11303. An isolated imperfect femur. Buffelsvlei, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

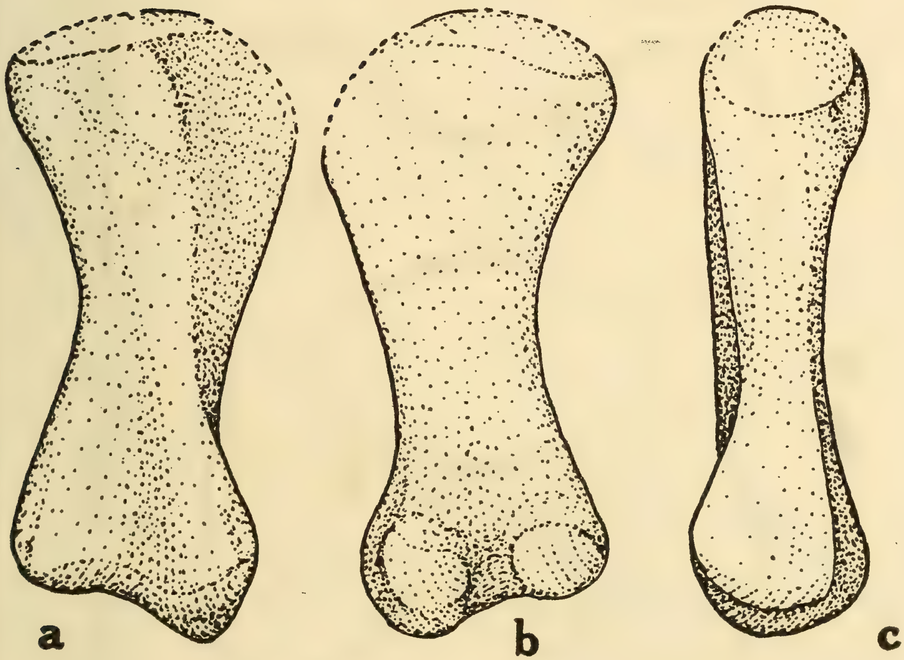
S.A.M. 11306. An isolated good femur (Fig. 11), which agrees well with the proximal end of the femur (B.M. 43525) which I am including in the type material of *Phocosaurus*.

The femur is quite robust and fairly long (498 mm.); the width over the external trochanter is moderate (234 mm.); the preaxial face is concave, with the caput directed well preaxially; the caput is massive (164 × 114 mm.); the shaft is fairly long and narrow (diams. 120 × 86 mm.); the tibial facets are

directed much distally and the postaxial epicondyle lies further distally than the preaxial epicondyle; the femoro-tibialis ridge is fairly strong and the area for the insertion of the ilio-femoralis is narrow.

Boesmansrivier, Beaufort West. Mid *Tapinocephalus* zone. Coll. Boonstra.

Fig. 11.



Femur of ? *Phocosaurus*. (× ⅛.) S.A.M. 11306. a. Dorsal view. b. Ventral view. c. Anterior view.

S.A.M. 11702. An isolated distal end of a humerus (Fig. 12 b-d) which agrees fairly well with that of *Tapinocephalus*. Elandsberg, Sutherland. Low? *Tapinocephalus* zone. Coll. Boonstra.

S.A.M. 11993. An isolated good left humerus (Fig. 13) with a long delto-pectoral crest and a well-modelled radial condyle as in *Phocosaurus*, but otherwise much like the humerus of *Tapinocephalus*. Locality and collector unknown.

S.A.M. 11997. An incomplete ilium (Fig. 14), distal end of a femur and the distal end of a radius, associated with a fairly good but as yet unprepared skull.

Fig. 12.

a b c d

Humeri of ? *Tapinocephalus*. ($\times \frac{1}{8}$.) a. S.A.M. 2753. Ventral view. b. S.A.M. 11702. Ventral view. c. S.A.M. 11702. Dorsal view. d. S.A.M. 11702. Anterior view.

The ilium has most of its blade missing, but on the lower edge of the posterior iliac process there is a strong ilio-fibularis ridge lying horizontally; the acetabulum is very large but shallow.

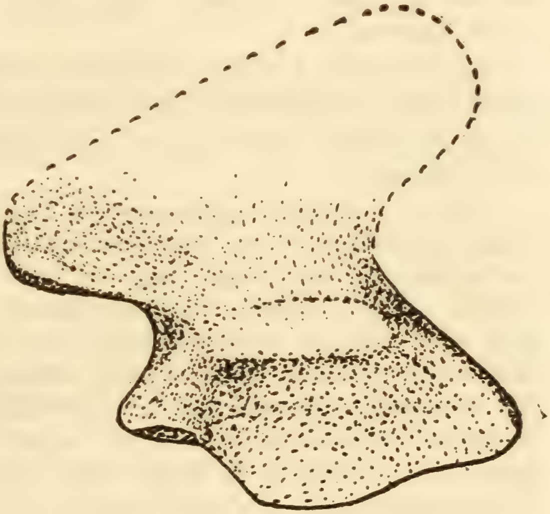
In its unprepared state the skull cannot be definitely identified; it is certainly not that of *Keratocephalus* and in shape differs from that of *Tapinocephalus* and may thus very possibly be near *Phocosaurus*.

Locality and collector unknown.

Fig. 13.

Humerus of ? *Tapinocephalus*. (× ⅛.) S.A.M. 11993. Ventral view.

Fig. 14.



Ilium of ? *Phocosaurus*. (× ⅛.) S.A.M. 11997. Lateral view.

Struthiocephalidae

Family Characters of the Girdles and Limbs.

With much more material at our disposal than in the case of the Tapinocephalidae a much fuller account can be given of the girdles and limbs of the Struthiocephalidae.

The pectoral girdle is small to medium sized and light to only fairly massive.

The scapula is small and low (310 mm.) to fairly large and high (480-500 mm.) with the upper part of the blade expanded (120-230 mm.); its posterior border is fairly concave; the tricipital ridge is not very strongly developed; the subscapular groove is shallow and confluent with a groove lying in the visceral face of the precoracoid, dorsally of the inner opening of the supracoracoid canal; the glenoidal facet of the scapula is of medium size, concave and with a fairly well-moulded and raised external rim and it faces postero-ventrally but not externally.

The coracoidal plate is long antero-posteriorly. The precoracoid is fairly large and consists of a fairly thin plate of bone, but is thickened at the apex, which lies dorso-posteriorly of the outer opening of the supracoracoid foramen; its outer face is only very slightly convex; the supracoracoid canal is not directed very obliquely and its inner opening still lies in the precoracoid near the precoracoid-scapular suture, but has a groove dorsally confluent with the subscapular groove. The precoracoid is excluded from the glenoid and on the apex it carries a ridge which limits the anterior movement of the humerus.

The coracoid is a fairly strong element with a fairly large glenoidal facet which faces dorso-posteriorly and also externally.

No cleithrum is preserved but in all probability was a splintlike bone as in *Moschops*.

A pair of clavicles is preserved in *Struthiocephalus whaitsi*, but as is evident from Fig. 17 they have suffered from distortion, so that the right one appears to be a much squatter bone than the left one. The left clavicle, which I believe shows the natural form more truly, is a fairly light bone with an expanded lower end, which is applied to the outer face of the upturned interclavicular antero-lateral corner; the upper end has its anterior edge thickened and posteriorly there is a thin flange, which is applied to the outer face of the scapula; internally a ridge limits the posterior movement of the clavicle over the scapula.

The interclavicle is a strong bone with a fairly thick and long stem, which is, however, only moderately wide; the anterior spatulate end is considerably expanded and curves strongly upwards; the moderately hollowed surface for the reception of the clavicle is dorso-posteriorly bounded by the thickened raised edge of the bone; the upper surface of the stem has no median ridge for the lower edge of the coracoidal plate to abut against.

The humerus of this family varies considerably; in some cases it is fairly short and broad and in others long and fairly slender; in length it varies from small to fairly large (276?-475 mm.); the proximal expansion is moderate to large (156-270 mm.); the distal expansion is moderate to very large (174-288 mm.); the shaft is short to long and narrow to very broad

(width 84-125 mm.); the delto-pectoral crest is short to fairly long and it terminates, in all cases, well proximal to the plane in which the ventral opening of the entepicondylar foramen lies; the caput is narrowly to moderately narrowly oval; both the processus medialis and the processus lateralis lie far proximally, more or less in the same plane as the caput; the radial condyle is weak, not well modelled, and does not extend much proximally along the ventral surface and thus always lies well distal of the plane in which the entepicondylar foramen lies; the twist on the shaft is small to moderate (8°—20°) and the one case in which it is 50°, this is undoubtedly due to postmortem distortion; the L.M.L. is weak to fairly strong; the A.D.V.L. is moderately to well developed; the entepicondyle is weak to moderate and the foramen slitlike; the ectepicondyle is little to greatly expanded.

The ulna is very inadequately known and is apparently fairly light and relatively long (258-366? mm.).

The radius is only known from a couple of ends.

The pelvis, hitherto unknown except for Haughton's (20) photograph of the mounted skeleton of *Struthiocephalus* and Broom's (15) restoration sketch based on it, is represented in the collection by three fairly well preserved specimens and a fourth with two iliae. The three bones of the pelvis are weakly united and the symphysis between the two halves is weak.

The pubo-ischiadic plate is relatively fairly long (the antero-posterior length is 90-102% of the height ot the pelvis); the supra-acetabular part of the ilium is low (45-65% of its antero-posterior length) and long antero-posteriorly; the anterior process of the ilium is long and low and only slightly everted; the posterior process of the ilium is not much shorter than the anterior process, but is much lower, with its posterior edge lying nearly horizontally and partially everted to form a weak ridge (for the insertion of the m. ilio-fibularis), which also lies nearly horizontally; the dorsal iliac edge is folded over laterally to overhang and limit the gluteal area; on the inner face of the anterior iliac process there is a strong attachment of a rib anterior to the main sacral rib. In the pubis the upper part of the anterior edge is strongly everted to form an elongated tuberculum pubis, which is ventrally demarcated from the slightly thickened antero-ventral edge by a distinct step; in the median line the middle part of the pubis meets its fellow in a very weak pubic symphysis; the middle part of the ventral edge of the ischium is thickened to form a large sutural face for a fairly strong ischial symphysis; between the pubic and ischial symphyses there is a large quadrangular fenestra, in life filled with cartilage.

The femur of the Struthiocephalidae shows considerable variation: small (length 276 mm.), light and slender or medium sized (length 408-440 mm.),

fairly robust and broad or fairly long (468 mm.), fairly light and fairly slender; the width over the external trochanter is small (95 mm.) to great (210 mm.); the preaxial face is moderately to strongly concave with the caput only slightly or moderately preaxially directed; the external trochanter is not separated from the proximal face by any notch; the internal trochanter is undeveloped or forms a strong elongated tubercle, situated well away from the preaxial border; the shaft is fairly long to short and fairly slender to broad (55-125 mm.); the tibial facets are much distally directed; the m. femoro-tibialis originates on a fairly strong ridge; the ilio-femoralis area of insertion is narrow or broad.

The tibia is small (length 180 mm.) and slender to medium sized (length 240-270 mm.) and fairly slender with a well-developed cnemial ridge or eminence, and cnemial groove.

The fibula is light, fairly short to long and slender (228-288 mm.).

Genus *Struthiocephalus* Haughton

The pectoral girdle is of medium size and only fairly massive (total height as projected on to the median plane 696 mm.). The scapula is fairly massive and high (480 mm.); its posterior border is deeply concave. As the family description is based mainly on specimens of this genus refer back for additional characters of the pectoral girdle.

The humerus is preserved in two specimens with skulls associated, but in one, in addition to being juvenile, the humerus has undergone considerable postmortem distortion and in the other proximo-distal compression has shortened the bone with concomitant widening.

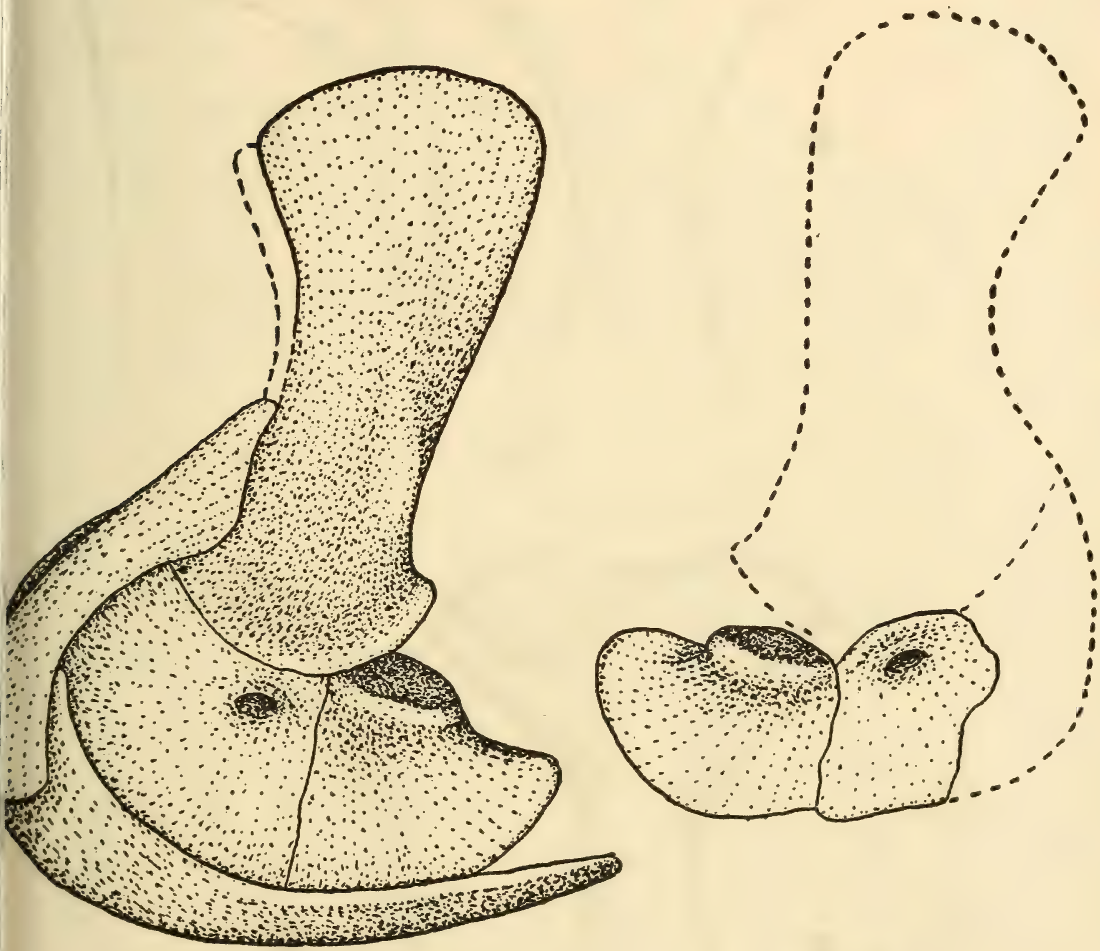
The humerus is fairly large (length 393-430 mm.) and fairly massive; the proximal expansion is large (270 mm.) and the distal expansion very large (288 mm.); the shaft is fairly long to short, moderately thick (diams. 102 × 60 mm.) to robust (diams. 126 × 60 mm.); the delto-pectoral crest is of medium length, terminating fairly far proximal of the ventral opening of the entepicondylar foramen; the caput is narrowly oval and lies slightly proximal to the processus medialis; the twist on the shaft is moderate (20°; in the deformed S.A.M. 11493 it is 50°); the L.M.L. is fairly strong; the A.D.V.L. is well developed; the entepicondyle is fairly strong with the foramen entering dorso-postaxially and leaving as a ventral slit; the ect-epicondyle is greatly expanded as a thin sheet of bone.

The ulna and radius are inadequately known.

The pelvis is as described for the family; it may be noted here that in both specimens known, but in particular in the juvenile one, the ilium has not grown out to meet the other two bones in the central part of the

acetabulum, whereas the three bones meet in the pelvis of *Struthiocephalellus* which on account of its small size might have been considered a not fully grown *Struthiocephalus*.

Fig. 15.

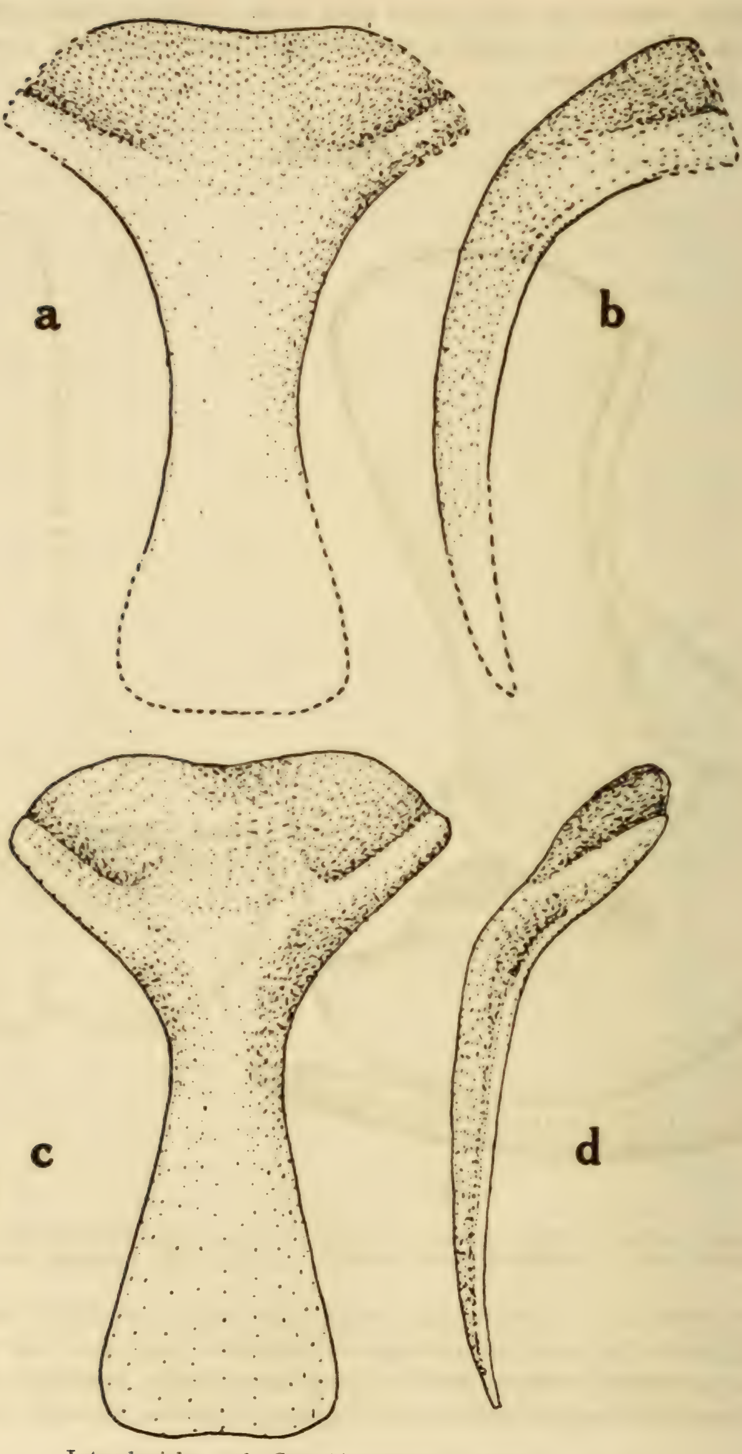


a b

a. Pectoral girdle of *Struthiocephalus whaitsi*. S.A.M. 3012. Lateral view. (× ⅛.)
b. Coraco-scapula of *Struthiocephalus whaitsi*. S.A.M. 11493. Lateral view. (× ⅛.)

The femur is of medium size (length 440 mm.) and fairly broad and robust; the width over the external trochanter is 204 mm.; the preaxial face is moderately concave and the caput only slightly preaxially directed; the internal trochanter forms a fairly strong ridgelike tubercle; the shaft

Fig. 16.



Interclaviclae of *Struthiocephalus whaitsi*. (× ⅛.) a. S.A.M. 3012. Ventral view. b. S.A.M. 3012. Lateral view. c. S.A.M. 11579. Ventral view. d. S.A.M. 11579. Lateral view.

short and broad (diams. 125 × 50 mm.); as preserved the postaxial tibial facet lies much distally; the ilio-femoralis area of insertion is broad.

The tibia appears to be fairly short (240 mm.).

The fibula is fairly short (230 mm.) but fairly robust with a deeply concave preaxial border.

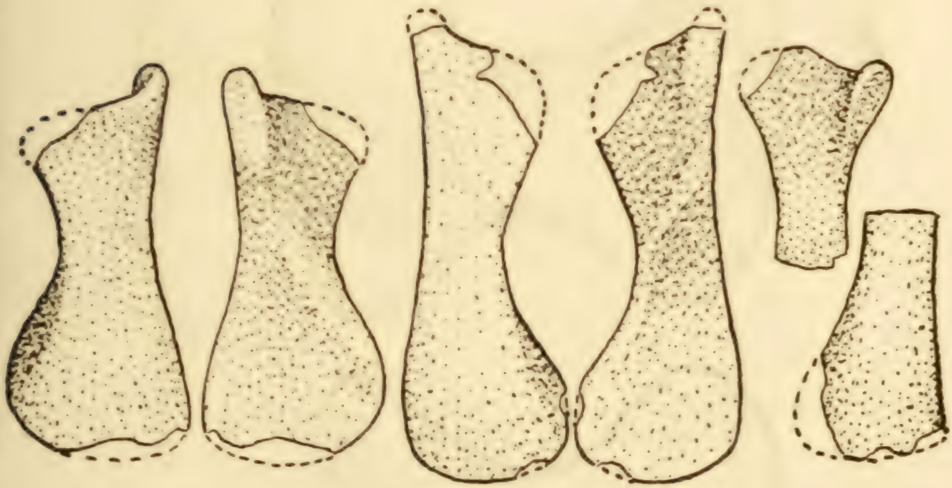
Struthiocephalus whaitsi Haughton

The specific description is as for the genus.

Referred specimens in the S.A.M. collection:

S.A.M. 3012. A nearly complete and fairly good pectoral girdle (Figs. 15a, 16 a-b and 17 a-d), a good humerus (Fig. 18), a fairly good pelvis (Fig. 19), two somewhat crushed femora (Fig. 20), a fair tibia (Fig. 21) and fibula (Fig. 22), associated with a fairly good but crushed skull. Abrahamskraal, Prince Albert. Low *Tapinocephalus* zone. Coll. Haughton.

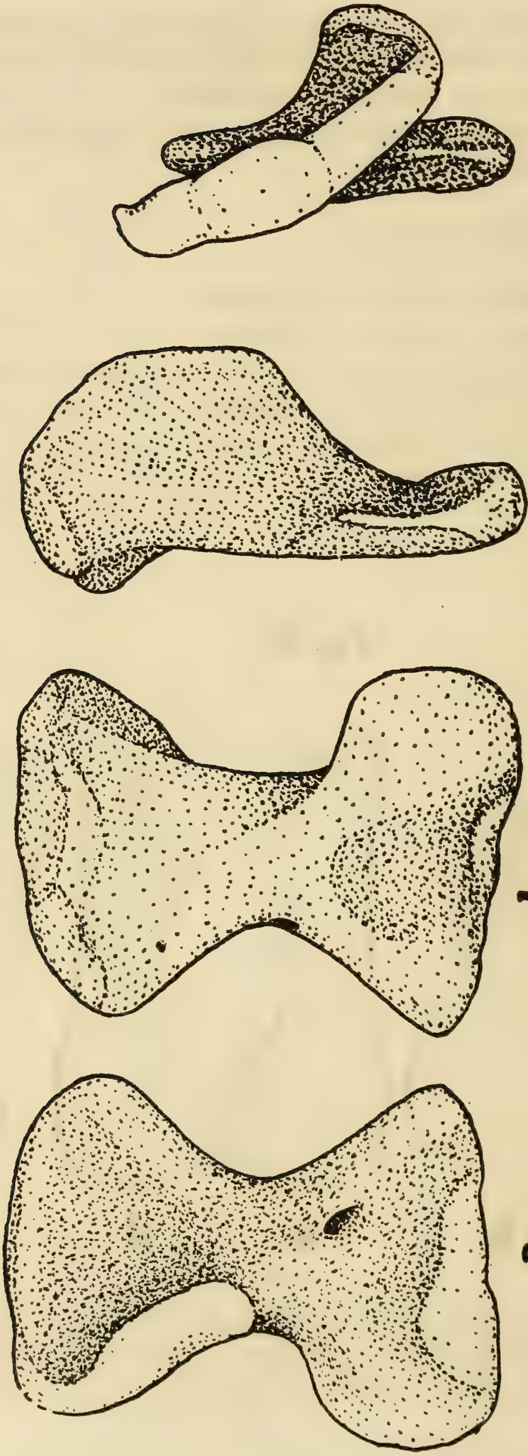
Fig. 17.



a b c d e

Claviculae. (× ¼.) a. *Struthiocephalus whaitsi*. S.A.M. 3012. Lateral view of right clavicle. b. *Struthiocephalus whaitsi*. S.A.M. 3012. Inner view of right clavicle. c. *Struthiocephalus whaitsi* S.A.M. 3012. Lateral view of left clavicle. d. *Struthiocephalus whaitsi*. S.A.M. 3012. Inner view of left clavicle. e. *Moschops capensis*. S.A.M. 11972. Inner view of left clavicle.

Fig. 18.

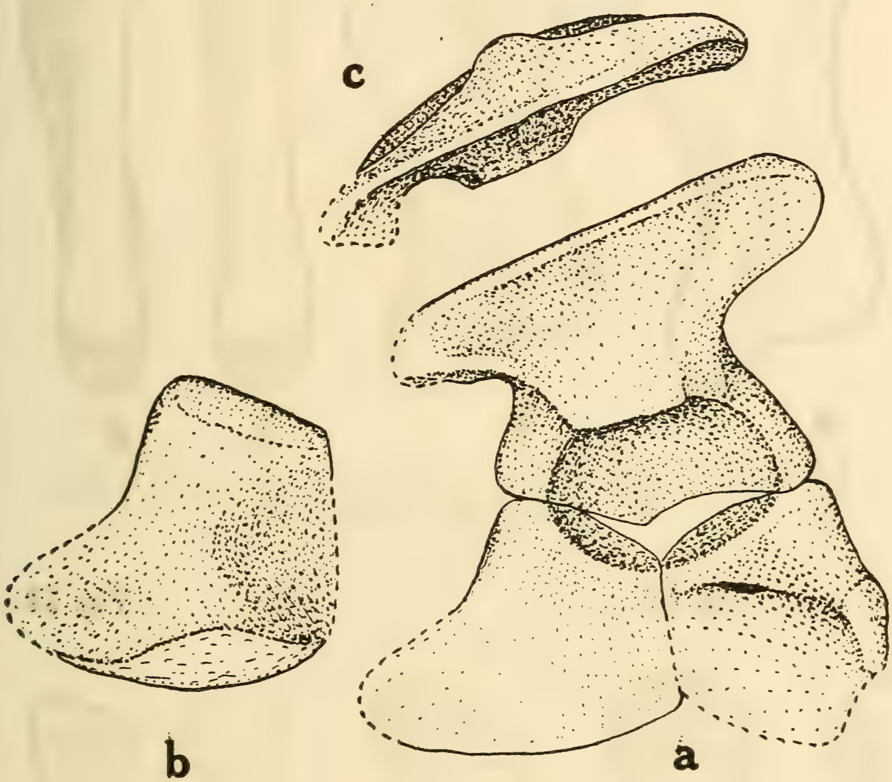


a b c d

Humerus of *Struthiocephalus whaitsi.* S.A.M. 3012. (× ¼.) a. Ventral view. b. Dorsal view. c. Anterior view. d. Proximal view.

S.A.M. 11493. A fair coracoidal plate (Fig. 15b), a distorted humerus (Fig. 23) and a good pelvis (Figs. 24 and 25), associated with a fairly good skull. Juvenile. Mynhardtskraal, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

Fig. 19.

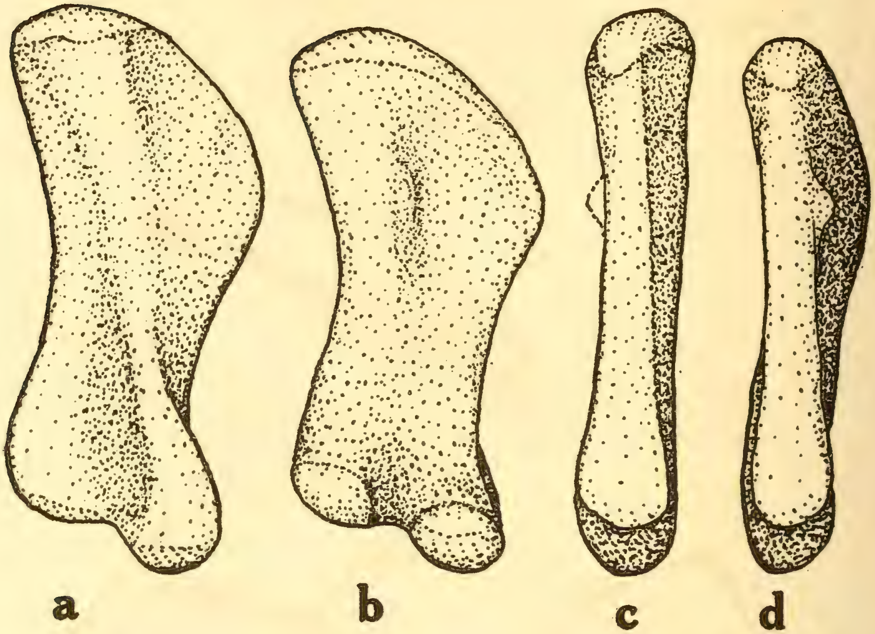


Struthiocephalus whaitsi. S.A.M. 3012, ($\times \frac{1}{8}$.) a. Pelvis in lateral view. b. Ischium in inner view. c. Ilium in dorsal view.

S.A.M. 11572. A fair interclavicle, most of both coracoidal plates and the proximal ends of both scapulae (Fig. 26). Klein-Koedoeskop, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

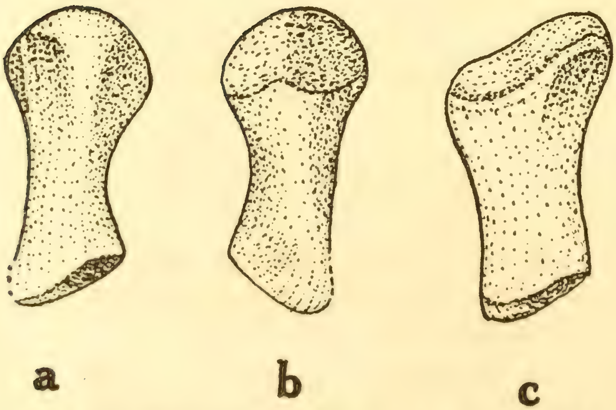
S.A.M. 11579. A good proximal two-thirds of a humerus, a good precoracoid and a good interclavicle (Fig. 16 c-d). Buffelsvlei, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

Fig. 20.



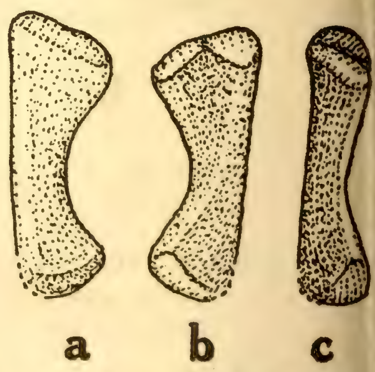
Femora of *Struthiocephalus whaitsi*. S.A.M. 3012. (× ⅛.) a. Left femur in dorsal view. b. Right femur in ventral view. c. Left femur in anterior view. d. Right femur in anterior view.

Fig. 21.



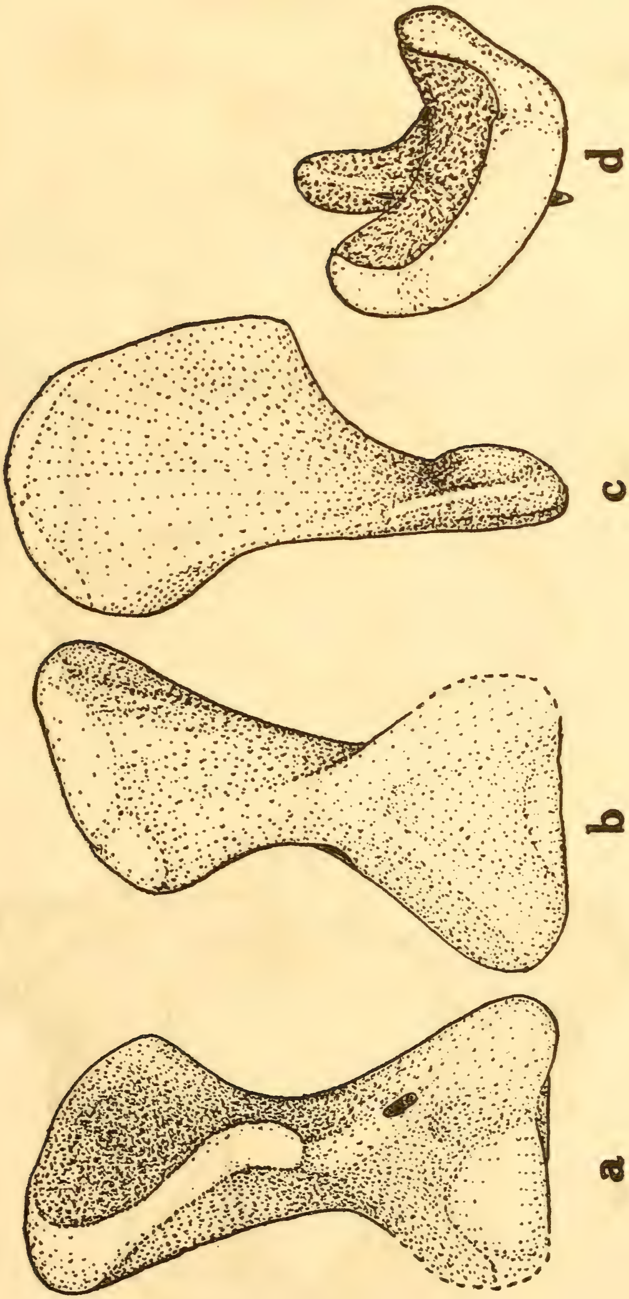
Tibia of *Struthiocephalus whaitsi*. S.A.M. 3012. (× ⅛.) a. Dorsal view. b. Ventral view. c. Posterior view.

Fig. 22.



Fibula of *Struthiocephalus whaitsi*. S.A.M. 3012. (× ⅛.) a. Dorsal view. b. Ventral view. c. Anterior view.

Fig. 23.



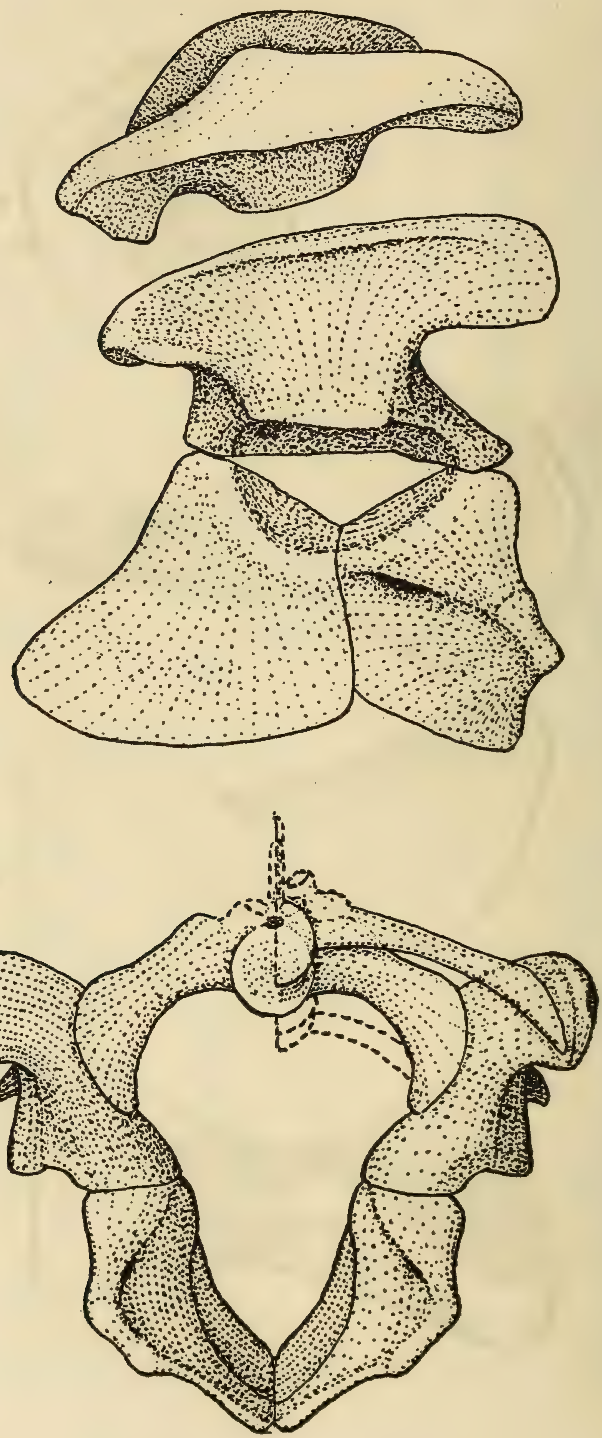
Humerus of a juvenile *Struthiocephalus whaitsi*. S.A.M. 11493. ($\times \frac{1}{8}$.) a. Ventral view. b. Dorsal view. c. Anterior view. d. Proximal view.

Fig. 24.

a

b

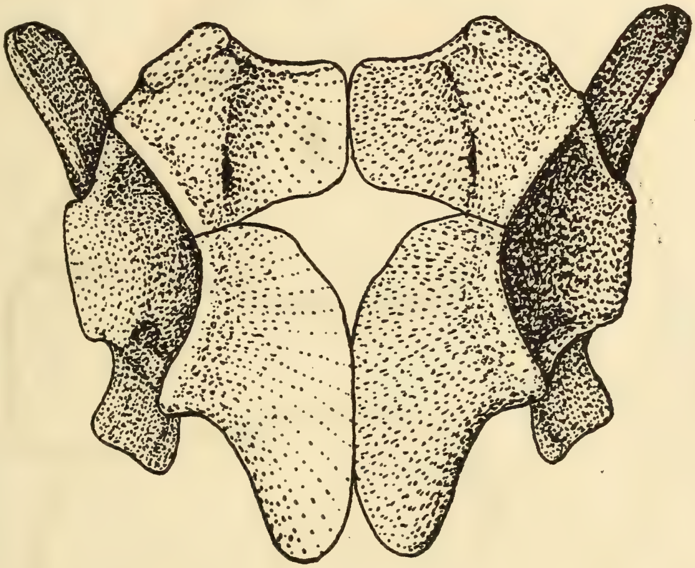
c



Struthiocephalus whaitsi. Juvenile. S.A.M. 11493. (× $\frac{1}{8}$.)
a. Ilium in dorsal view. b. Pelvis in lateral view. c. Pelvis in anterior view.

S.A.M. 11939. A weathered humerus, ulna (Fig. 27 a-b) and femur (Fig. 27 d-f), associated with a jaw fragment. Dikbome, Laingsburg. Low *Tapinocephalus* zone. Coll. Boonstra.

Fig. 25.



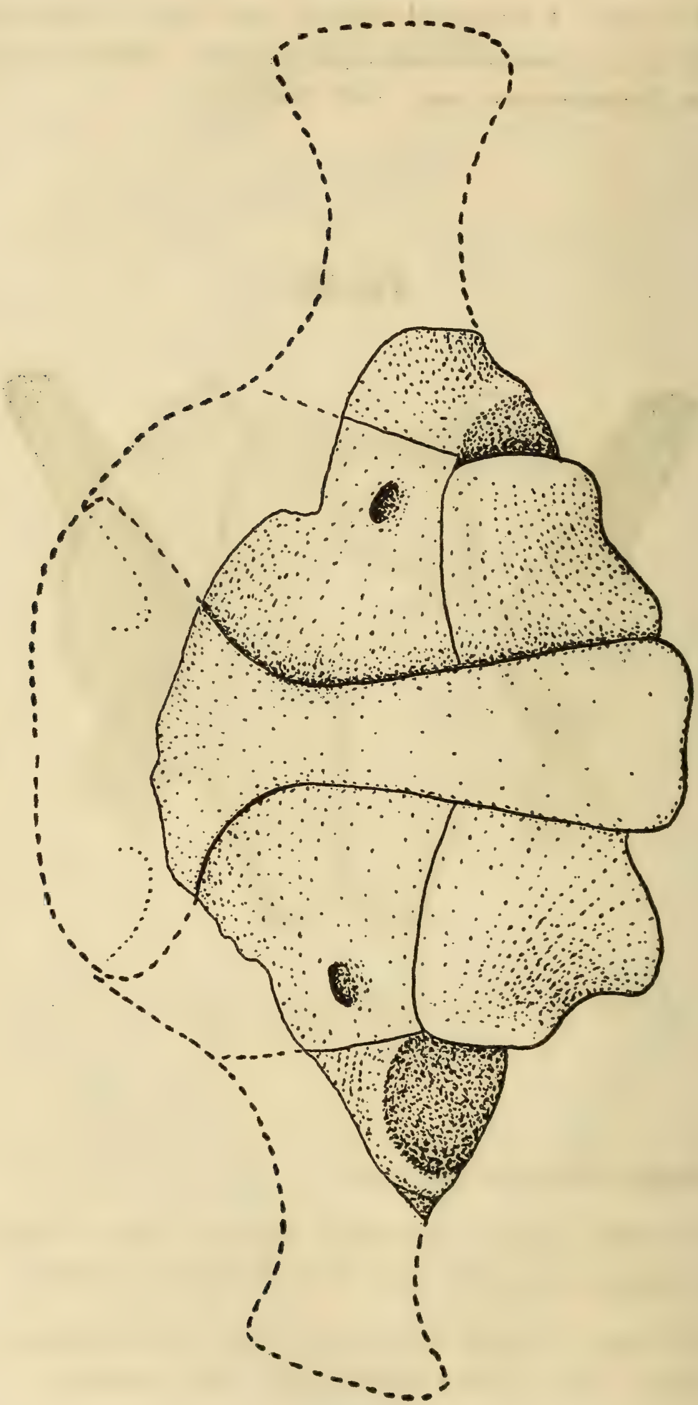
Pelvis of *Struthiocephalus whaitsi*. Juvenile. S.A.M. 11493. (× ⅛.) Ventral view.

Specifically undetermined specimen:

The following specimen approaches sufficiently close to warrant provisional inclusion in the genus, but not in the species — *whaitsi*.

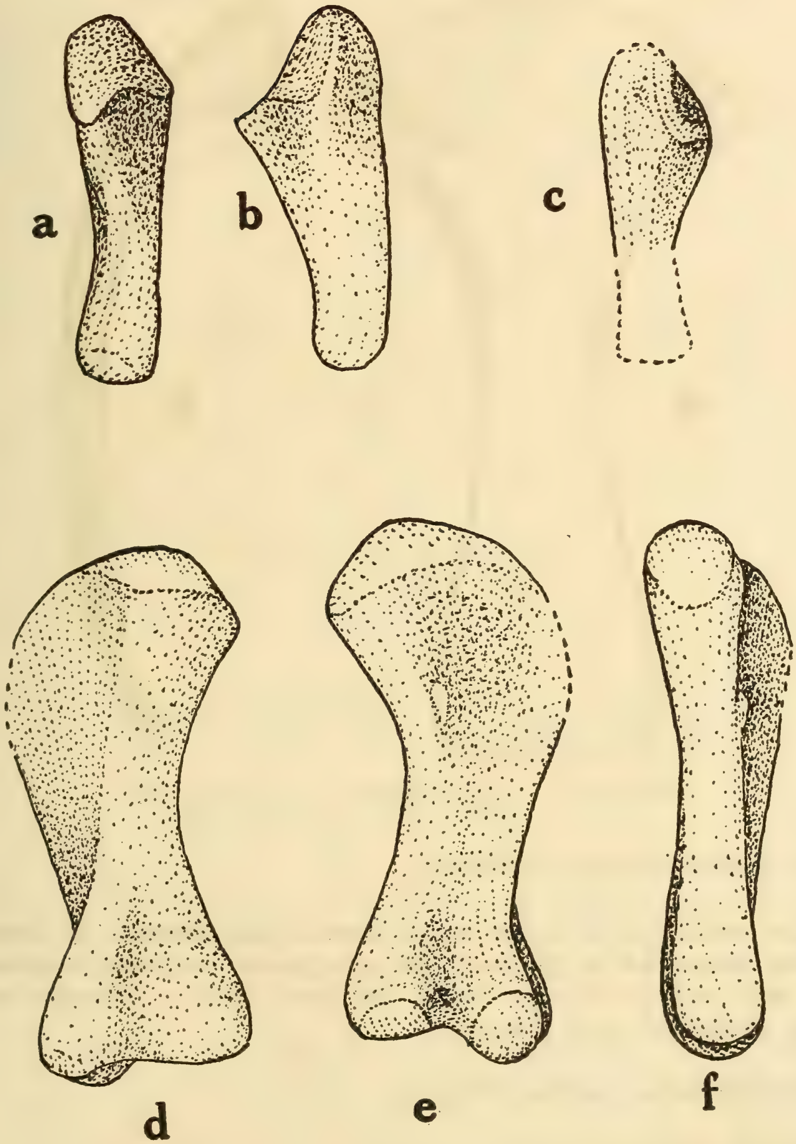
S.A.M. 11941. A good interclavicle (Fig. 28). Droëfontein, Prince Albert. Low ? *Tapinocephalus* zone. Coll. Boonstra.

Fig. 26.



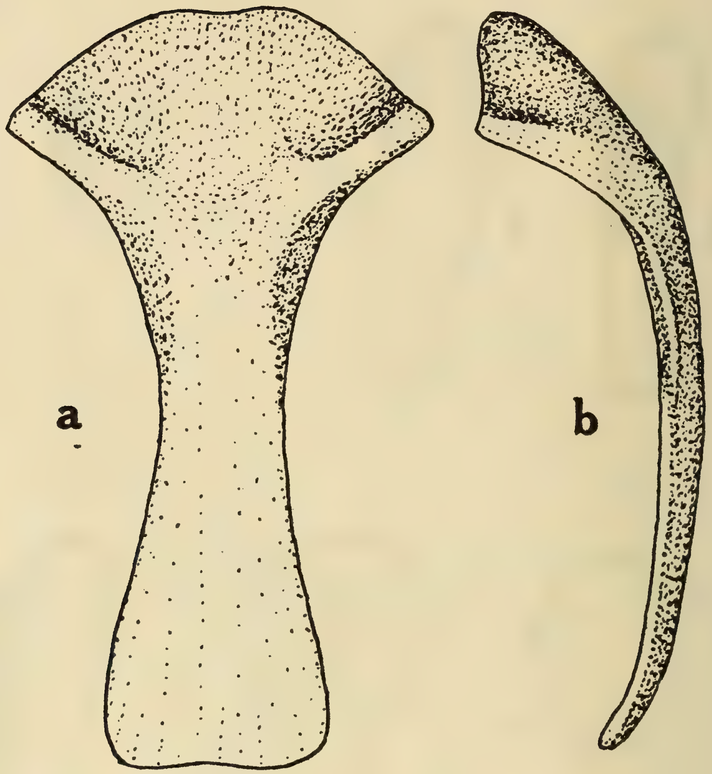
Pectoral girdle of *Struthiocephalus whaitsi*. S.A.M. 11572. (× $\frac{1}{8}$.) Ventral view.

Fig. 27.



a. Ulna of *Struthiocephalus whaitsi*. S.A.M. 11939. Dorsal view. (× $\frac{1}{6}$.)
b. Ulna of *Struthiocephalus whaitsi*. S.A.M. 11939. Anterior view. (× $\frac{1}{6}$.)
c. Ulna of *Struthiocephalus parvus*. S.A.M. 5006. Dorsal view. (× $\frac{1}{6}$.)
d. Femur of *Struthiocephalus whaitsi*. S.A.M. 11939. Dorsal view. (× $\frac{1}{6}$.)
e. Femur of *Struthiocephalus whaitsi*. S.A.M. 11939. Ventral view. (× $\frac{1}{6}$.)
f. Femur of *Struthiocephalus whaitsi*. S.A.M. 11939. Anterior view. (× $\frac{1}{6}$.)

Fig. 28.



Interclavicle of *Struthiocephalus sp.* S.A.M. 11941.
(× ⅛.) a. Ventral view. b. Lateral view.

Genus *Struthiocephaloides* Boonstra

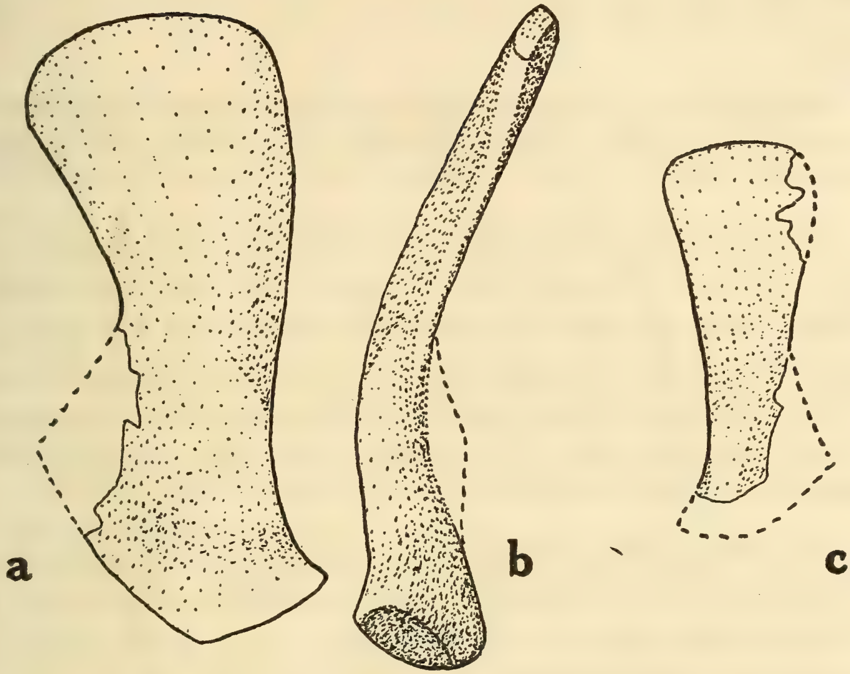
The pectoral girdle is only known from a single scapula; the scapula is fairly large and high (500 mm.); the upper part of the blade is expanded (210 mm.) and the posterior face is not deeply concave. No other part of the girdles and limbs is known.

Struthiocephaloides cavifrons Boonstra

Specific description as for the genus.

Type: S.A.M. 5607. A left scapula (Fig. 29 a-b), associated with a good skull. Lammerkraal, Prince Albert. High *Tapinocephalus* zone. Coll. Haughton.

Fig. 29.



Scapulae. (× ⅙.) a. *Struthiocephaloides cavifrons*. S.A.M. 5607. Lateral view. b. *Struthiocephaloides cavifrons*. S.A.M. 5607. Posterior view. c. *Struthiocephalellus parvus*. S.A.M. 5006. Lateral view.

Genus *Struthiocephalellus* Boonstra

The pectoral girdle is only known from an imperfect scapula and fragments of the coracoidal plate; the scapula is small (height 310? mm.) and the width of the blade is 210? mm.; the posterior face of the scapula is only slightly concave.

The humerus is small (length 276? mm.) and is lightly built; the proximal expansion is fairly great (156 mm.); the distal expansion is relatively great (174 mm.); the shaft is fairly long and fairly wide (diams. 66 × 48 mm.); the delto-pectoral crest is only moderately long and is fairly weak and terminates well proximal of the plane in which the ventral opening of the entepicondylar foramen lies; the relations of caput, processus medialis and lateralis are unknown; the radial condyle is weak (thickness 48 mm.), distally situated and curving round on to the dorsal surface; the twist on the

shaft is moderate (20° ?); the L.M.L. is weak and the A.D.V.L. fairly strong; the entepicondyle is expanded as a thin sheet of bone and the foramen enters ventro-postaxially and leaves as a ventral slit well away from the edge of the bone; the ectepicondyle is expanded as a thin curved sheet of bone.

The ulna has only the proximal part preserved; it is lightly built; proximal to the coronoid process a sharp longitudinal ridge separates a groove from the sigmoid surface; the ventral surface is deeply excavated longitudinally.

The pelvis has a relatively long pubo-ischiadic plate (97% of the height of the pelvis); the supra-acetabular part of the ilium is low (126 mm.) and long (200? mm. as restored) and the height is thus 63% of the length; although neither the anterior nor posterior iliac processes are fully preserved both appear to have been long and fairly low. The pubis is anteriorly slightly everted with a prominent tuberculum pubis, clearly demarcated from the medially directed antero-ventral edge of the pubis; the pubic symphysis is fairly long but is weak. The ischium is long with a long but weak symphysis; the postero-dorsal edge of the ischium is strongly thickened.

The femur is small, slender and fairly lightly built (length 276 mm.); the width over the external trochanter is small (95 mm.); the preaxial face is only slightly concave and the caput, which is relatively weak (55×25 mm.), is directed much dorsally as well as preaxially — there is thus a twist on the shaft; the external trochanter is indistinctly developed and the internal trochanter not developed at all; the shaft is long and fairly narrow and thin (diams. 55 × 48 mm.); the tibial facets face ventro-distally with the postaxial one lying further distally; the femoro-tibialis ridge is moderately strong and the ilio-femoralis area of insertion very narrow.

The tibia has its proximal face divided into two distinct concave facets by a sharp and strong dorso-ventral ridge; a prominent cnemial protuberance is present, continued distally as a sharp cnemial ridge, with a deep groove lying postaxially of this ridge; all these features are well and sharply modelled.

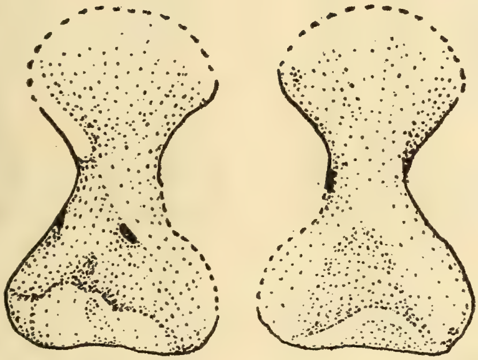
Struthiocephalellus parvus Boonstra

Type: S.A.M. 5006. A partial scapula (Fig. 29c), a fairly good humerus (Fig. 30), the proximal end of an ulna (Fig. 27c), a fairly good pelvis (Fig. 31), a good femur (Fig. 32) and the proximal end of a tibia (Fig. 33), associated with a fair skull. Abrahamskraal, Prince Albert. Low *Tapinocephalus* zone. Coll. Haughton.

Generically undetermined specimens:

S.A.M. 8947. This specimen, which consists of two fairly good femora (Fig. 34 a-c), a good tibia (Fig. 34 d-f) and a good fibula (Fig. 34 g-i), appears to be of a Struthiocephalid, larger and of somewhat heavier build than *Struthiocephalus whaitsi*. The tibia is noteworthy for its very strong cnemial protuberance. Mynhardtskraal, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

Fig. 30.



a b c

Humerus of *Struthiocephalellus parvus*. S.A.M. 5006. (× ⅛.) a. Ventral view. b. Dorsal view. c. Anterior view.

Fig. 31.

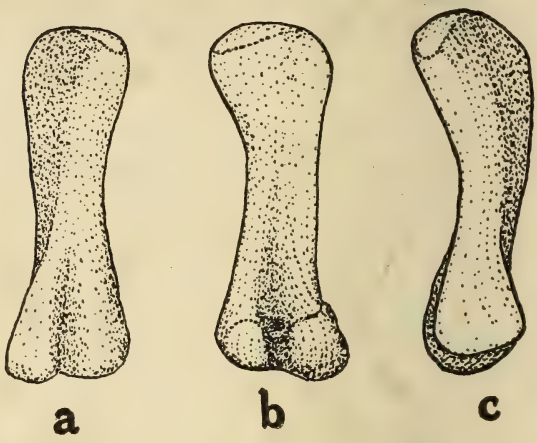
Pelvis of *Struthiocephalellus parvus*. S.A.M. 5006. (× ⅛.) Lateral view.

The following four specimens are of Struthiocephalids which are much longer in the limb than *Struthiocephalus*.

S.A.M. 3614. A good isolated humerus (Fig. 35 b-e). This humerus is relatively long and slender (length 480 mm.); both the proximal (width 192 mm.) and the distal (width 198 mm.) expansion is small; the shaft is fairly long and slender (diams. 95 × 78 mm.); the twist on the shaft is small (8°); the capitellum is very weakly modelled and situated far distally; both epicondyles are weak and the entry of the entepicon-

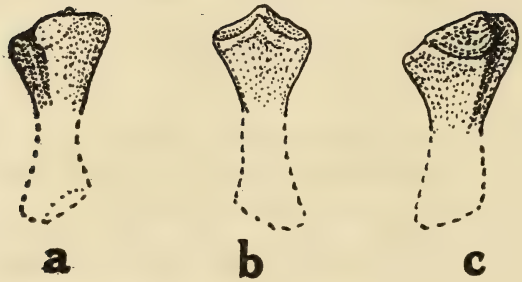
dylar foramen is clearly visible in dorsal view. Abrahamskraal, Prince Albert. Low *Tapinocephalus* zone. Coll. Haughton.

Fig. 32.



Right: Femur of *Struthiocephalellus parvus*. S.A.M. 5006. (× 1/8.) a. Dorsal view. b. Ventral view. c. Anterior view.

Fig. 33.



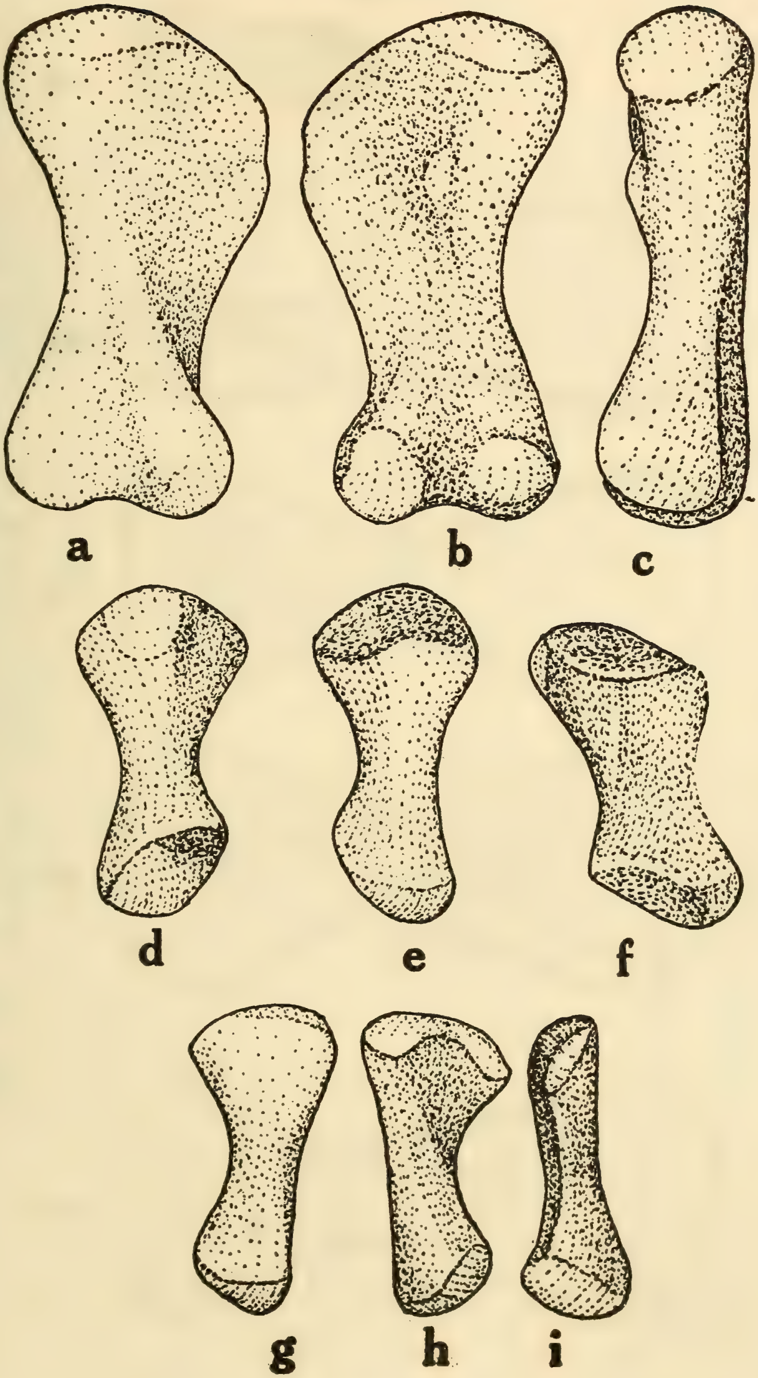
Left: Tibia of *Struthiocephalellus parvus*. S.A.M. 5006. (× 1/8.) a. Dorsal view. b. Ventral view. c. Posterior view.

S.A.M. 5009. A fair humerus with the proximal end not in contact with the shaft (Fig. 35a). Wolwefontein, Prince Albert. Low *Tapinocephalus* zone. Coll. Haughton.

Although the delto-pectoral crest is shorter than in S.A.M. 3614 and the processus medialis situated more nearly in the same plane as the caput these two specimens probably are of the same species.

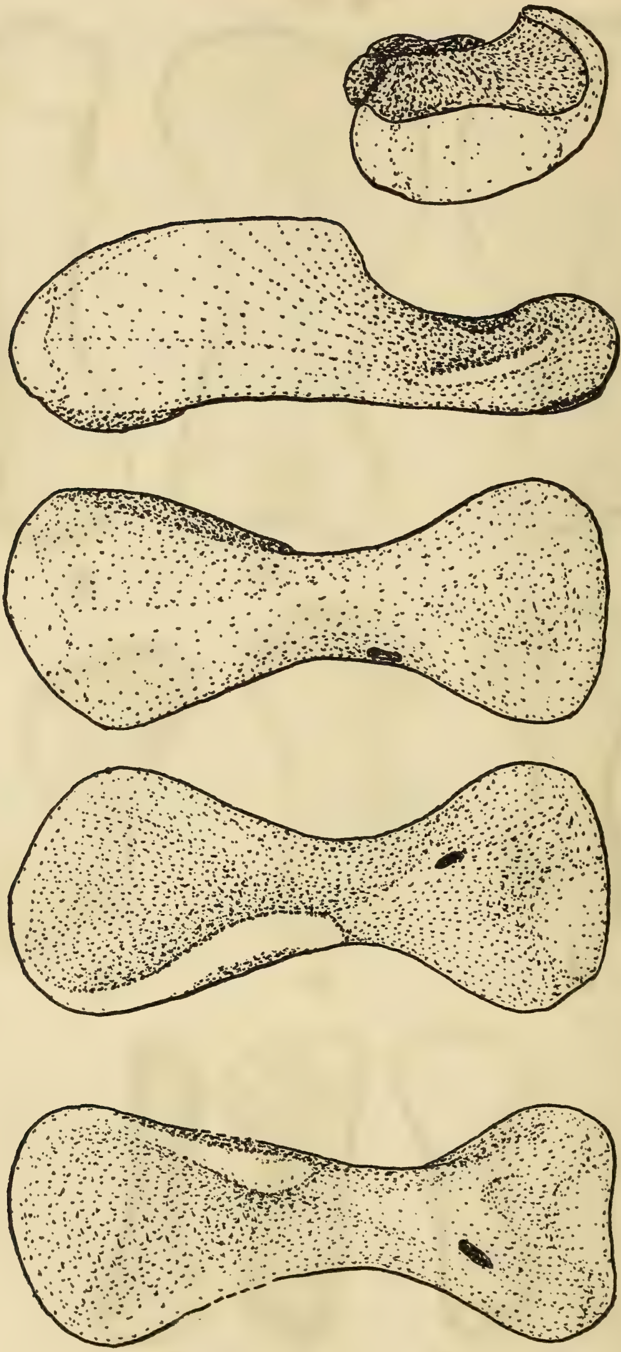
S.A.M. 4349. Two fairly good iliae (Fig. 36 a-b), a good femur (Fig. 36 c-e), the proximal halves of both ulnae (Fig. 36f) and of both tibiae and a fibula (Fig. 36g).

Fig. 34.



? *Struthiocephalus*. S.A.M. 8947. ($\times \frac{1}{8}$.) a. Femur in dorsal view. b. Femur in ventral view. c. Femur in anterior view. d. Tibia in dorsal view. e. Tibia in ventral view. f. Tibia in posterior view. g. Fibula in dorsal view. h. Fibula in ventral view. i. Fibula in anterior view.

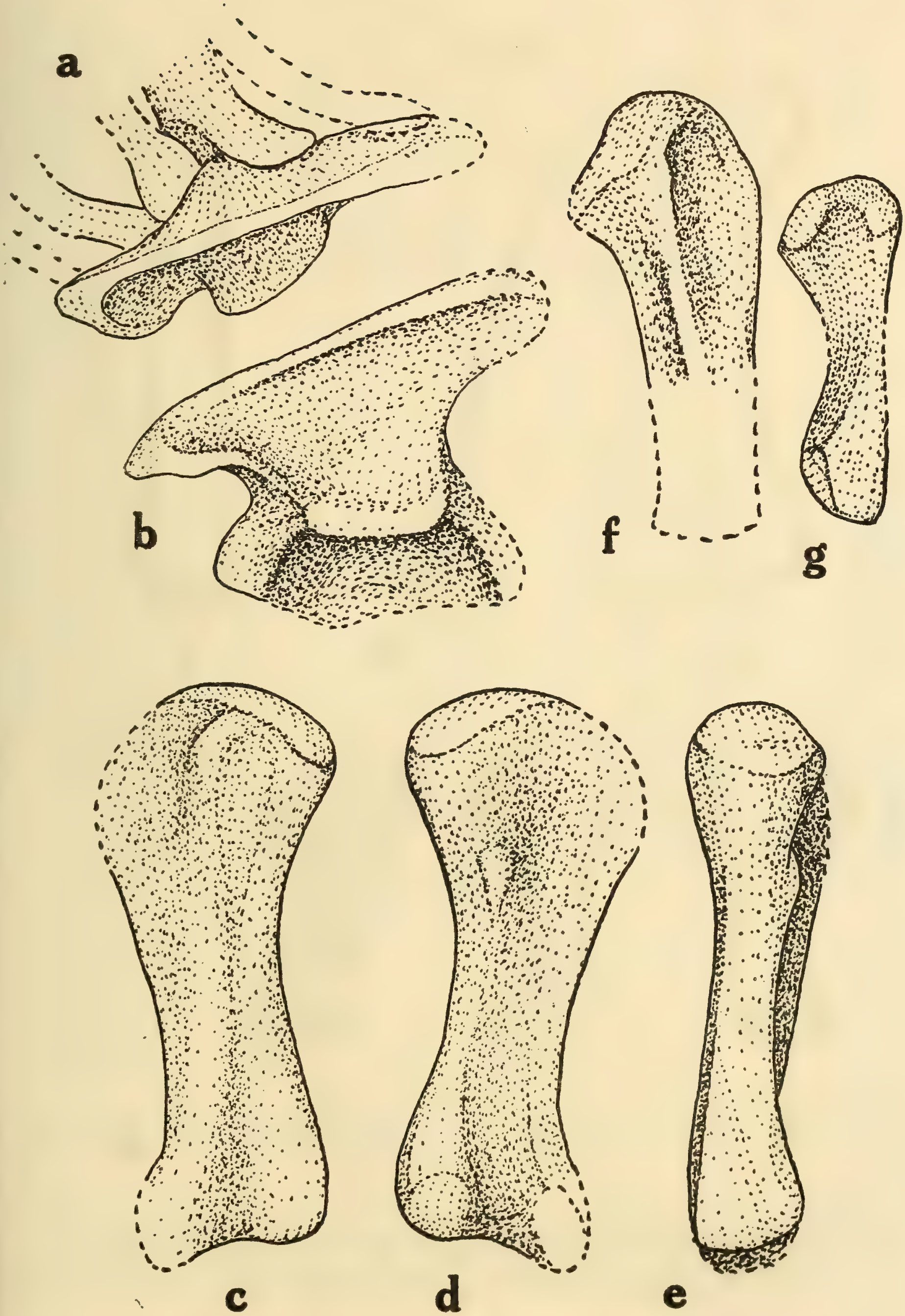
Fig. 35.



a b c d e

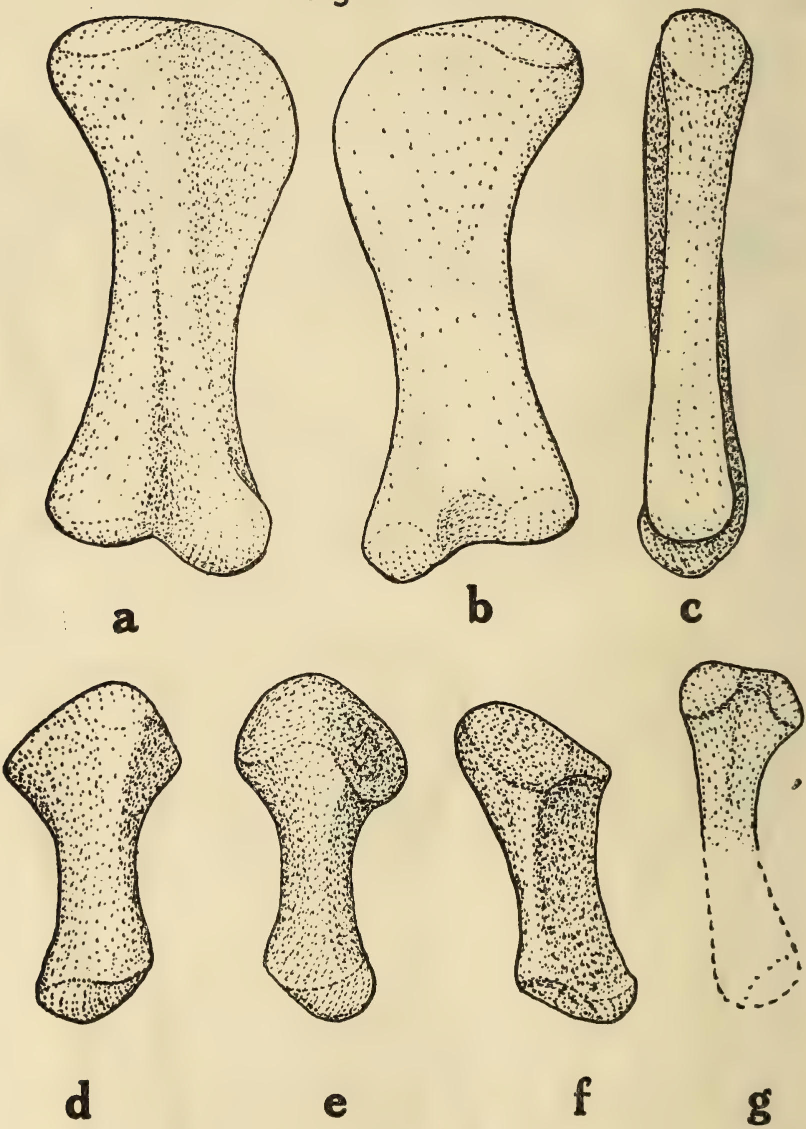
Humeri of an unnamed genus of the Struthiocephalidae. (× $\frac{1}{6}$.) a. S.A.M. 5009. Ventral view. b. S.A.M. 3614. Ventral view. c. S.A.M. 3614. Dorsal view. d. S.A.M. 3614. Anterior view. e. S.A.M. 3614. Proximal view.

Fig. 36.



An unnamed Struthiocephalid. S.A.M. 4349. (× $\frac{1}{8}$.) a. Ilium in dorsal view. b. Ilium in lateral view. c. Femur in dorsal view. d. Femur in ventral view. e. Femur in anterior view. f. Ulna in dorsal view. g. Fibula in ventral view.

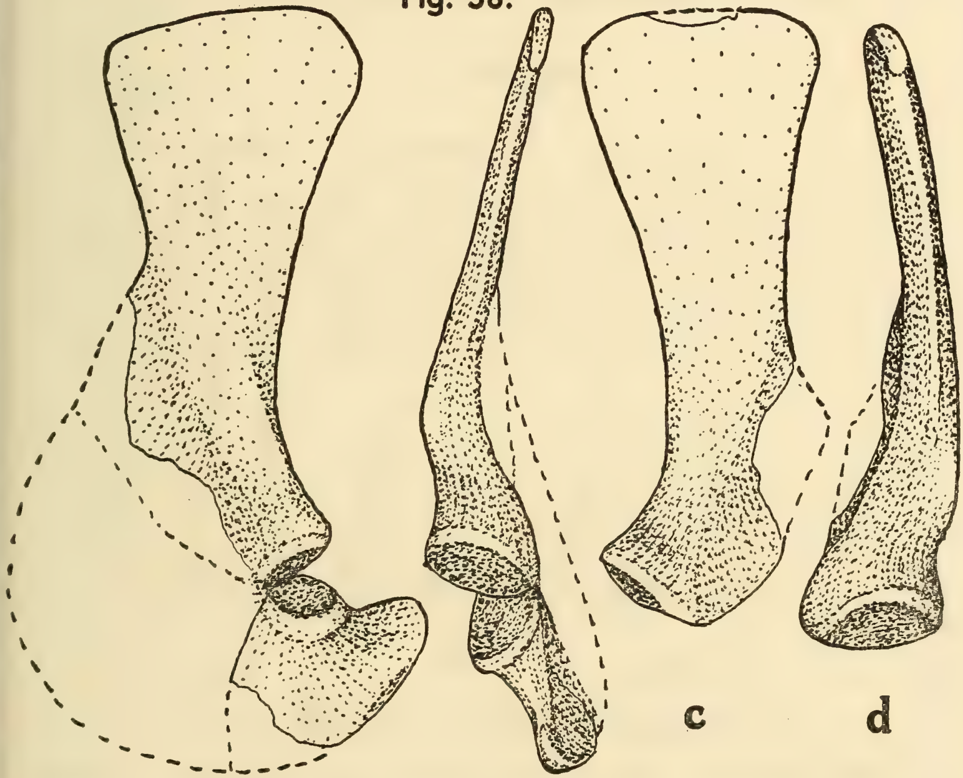
Fig. 37.



An unnamed Struthiocephalid. S.A.M. 9008 ($\times \frac{1}{6}$.) a. Femur in dorsal view. b. Femur in ventral view. c. Femur in anterior view. d. Tibia in dorsal view. e. Tibia in ventral view. f. Tibia in posterior view. g. Fibula in ventral view.

The ilium is low (supra-acetabular height 210 mm.), with both the anterior and the posterior process long and low (antero-posterior length 335? mm.); with the height thus 62% of the length; the anterior process is slightly everted and on its inner face receives a rib lying anterior to the main sacral rib; the origin of the m. ilio-fibularis lies on the everted horizontal ridge on the posterior iliac process; the dorsal edge of the ilium is folded over the upper limit of the gluteal area. It is thus apparent that this ilium is very similar to that of *Struthiocephalus*.

Fig. 38.



a b c d

Scapulae of two indetermined Struthiocephalids. (× 1/6.) a. S.A.M. 10197. Lateral view. b. S.A.M. 10197. Posterior view. c. S.A.M. 11700. Lateral view. d. S.A.M. 11700. Posterior view.

The femur is long (468 mm.) and slender; the width over the external trochanter apparently small (190? mm.); the preaxial face is quite strongly concave and the caput directed well preaxially; the internal trochanter is

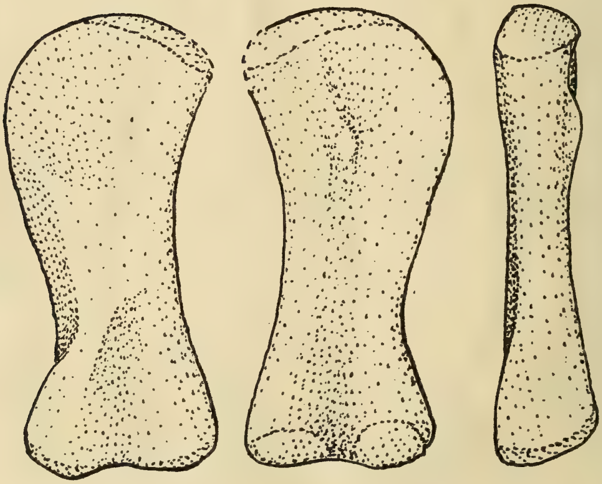
situated fairly near the preaxial border; the shaft is long and narrow (diams. 102 × 66 mm.); the tibial facets are directed well distally with the postaxial one situated furthest distally.

The ulna is apparently long with a strong longitudinal ridge and a deep excavation on its dorsal face. The tibia and fibula are both long and slender bones.

Leeurivier, Beaufort West. Low *Tapinocephalus* zone. Coll. Haughton.

S.A.M. 9008. A good femur (Fig. 37 a-c) and tibia (Fig. 37 d-f) and the proximal end of a fibula (Fig. 37g). Klein-Koedoeskop, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

Fig. 39.



a b c

Femur of uncertain affinity. S.A.M. 11880. (× $\frac{1}{6}$.)
a. Dorsal view. b. Ventral view. c. Anterior view.

This specimen is co-specific with S.A.M. 4349. These two specimens thus represent, together with S.A.M. 3614 and S.A.M. 5009, a Struthiocephalid with an ilium very similar to that of *Struthiocephalus* but with much longer pro- and epipodials.

The following two specimens both come from the Nieueveld, where the fauna of the *Tapinocephalus* zone is very poorly known.

S.A.M. 10197. An isolated well-preserved scapula and coracoid (Fig. 38 a-b). Grootfontein, Fraserburg. Low? *Tapinocephalus* zone. Coll. Boonstra.

S.A.M. 11700. A good isolated scapula (Fig. 38 c-d). Elandsberg, Sutherland. Low? *Tapinocephalus* zone. Coll. Boonstra.

These two scapulae are clearly Struthiocephalid and they may yet prove to be of one or other of the forms as yet only known from skulls (e.g. *Struthionops, Riebeeckosaurus* or the other species of *Struthiocephalus*).

S.A.M. 11880. An isolated femur (Fig. 39). The affinities of this bone are very doubtful; the tibial condyles are practically terminal and the internal trochanter situated well away from the preaxial border. Arthurskraal, Beaufort West. High? *Tapinocephalus* zone. Coll. Geol. Survey.

Moschopidae

Family Characters of the Girdles and Limbs.

The girdles and limbs of the Moschopidae are only moderately well represented in our collection. There are a good number of pectoral elements of *Moschops,* but of the pelvic girdle there is only a single ilium, and the pro- and epipodials reasonably represented. In drawing up the descriptions I have drawn upon the accounts of Broom (11), Romer (25) and Gregory (18) of the *Moschops* material in the American Museum.

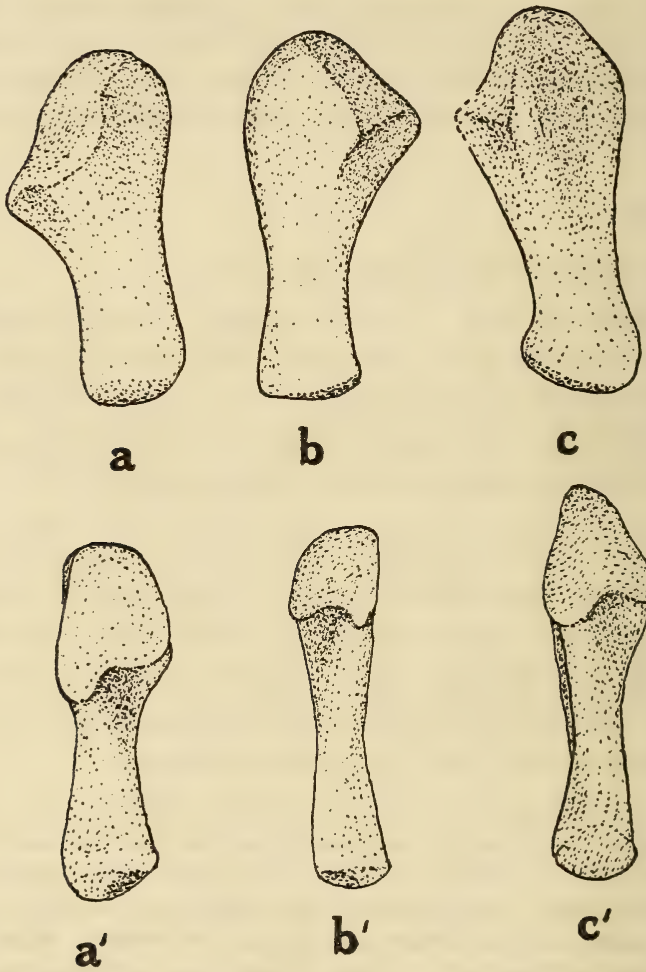
The pectoral girdle is lightly to fairly lightly built. The scapula is fairly low (400 mm.) to fairly high (440 mm.) or high (540 mm.) with the upper part of the blade broad (215 mm.) to fairly narrow (156-190 mm.); the posterior border is fairly straight; the tricipital ridge is moundlike, low and not very prominent; the canal for the supracoracoideus does not open directly into the subscapular groove, which, however, crosses the suture to meet the internal opening of the canal; the glenoidal facet of the scapula faces ventro-posteriorly, but not externally in *Avenantia*.

The coracoidal plate is not very long antero-posteriorly. The precoracoid is fairly large, but is mainly composed of a thin plate of bone which has its anterior edge only slightly thickened and its outer face moderately convex; the supra-coracoidal canal penetrates the bone very obliquely, so that its internal opening lies just below the precoracoid-scapular suture, with its upper rim notched and with a groove running into the subscapular groove; but in *Avenantia* the canal crosses the suture to open into the subscapular groove. The postero-dorsal apex of the precoracoid sometimes only just enters the anterior corner of the glenoid and here forms a slight depression in the ridge bounding the lateral edge of the glenoid.

The coracoid is small and light, but with a well-developed glenoidal facet, which faces postero-dorsally, but also well externally.

No cleithrum is preserved in any of my specimens, but if present could only have been a splintlike bone as found by Broom (11) in one of the Spitskop specimens.

Fig. 40.



Moschopid ulnae. ($\times \frac{1}{8}$.) a, a[1]. ? *Moschops*. S.A.M. 9124A in dorsal and anterior views. b, b[1]. ? *Moschops*. S.A.M. 9157, in dorsal and anterior views. c, c[1]. *Moschops capensis*. S.A.M. 11292, in dorsal and anterior views.

Of the clavicle only one dorsal and two ventral ends are preserved. Dorsally the posterior expansion overlying the scapula is relatively better developed than in *Struthiocephalus* and the *Titanosuchia*.

The interclavicle is a fairly large and strong bone, with a relatively long stem expanded posteriorly; anteriorly the spatulate end is not greatly expanded and the articulatory surface for the reception of the lower end of the clavicle is only slightly excavated, with the development of a slight groove in only one specimen. In my material the anterior end is not bent up as sharply as in the Spitskop material. There is no median ridge on the dorsal surface of the stem as in some *Titanosuchia*.

The humerus is moderately long (345-444 mm.); the proximal expansion is moderate to fairly large (170-240 mm.); the distal expansion is moderate (165?-240 mm.); the shaft is fairly long and moderately broad (width 78-91 mm.); the delto-pectoral crest is fairly short and its distal end lies well proximal of the ventral opening of the entepicondylar foramen; the caput is narrowly oval; both the processus medialis and the processus lateralis lie far proximally, more or less in the same plane as the caput; the radial condyle is fairly weak, not well modelled and it lies far distally and does not extend along the ventral face, and thus lies well distally of the entepicondylar foramen, but does curve a little round on to the dorsal face; the twist on the shaft is small to moderate (10-20°); the L.M.L. is moderately strong; the A.D.V.L. is distinct; the entepicondyle is moderately to fairly greatly expanded to form a thin curved sheet of bone, and the foramen is slitlike with its entrance visible in dorsal view on the dorso-postaxial border; the ectepicondyle is strongly expanded as a thin sheet of bone with ventrally, in some humeri, a well-marked groove functioning as does the ectepicondylar foramen in the Titanosuchids for the passage of the radial nerve.

The ulna is fairly light to moderate (length 275-300 mm.); the dorsal lip to the sigmoid face is weak to fairly strong; the styloid ridge is moderately strong.

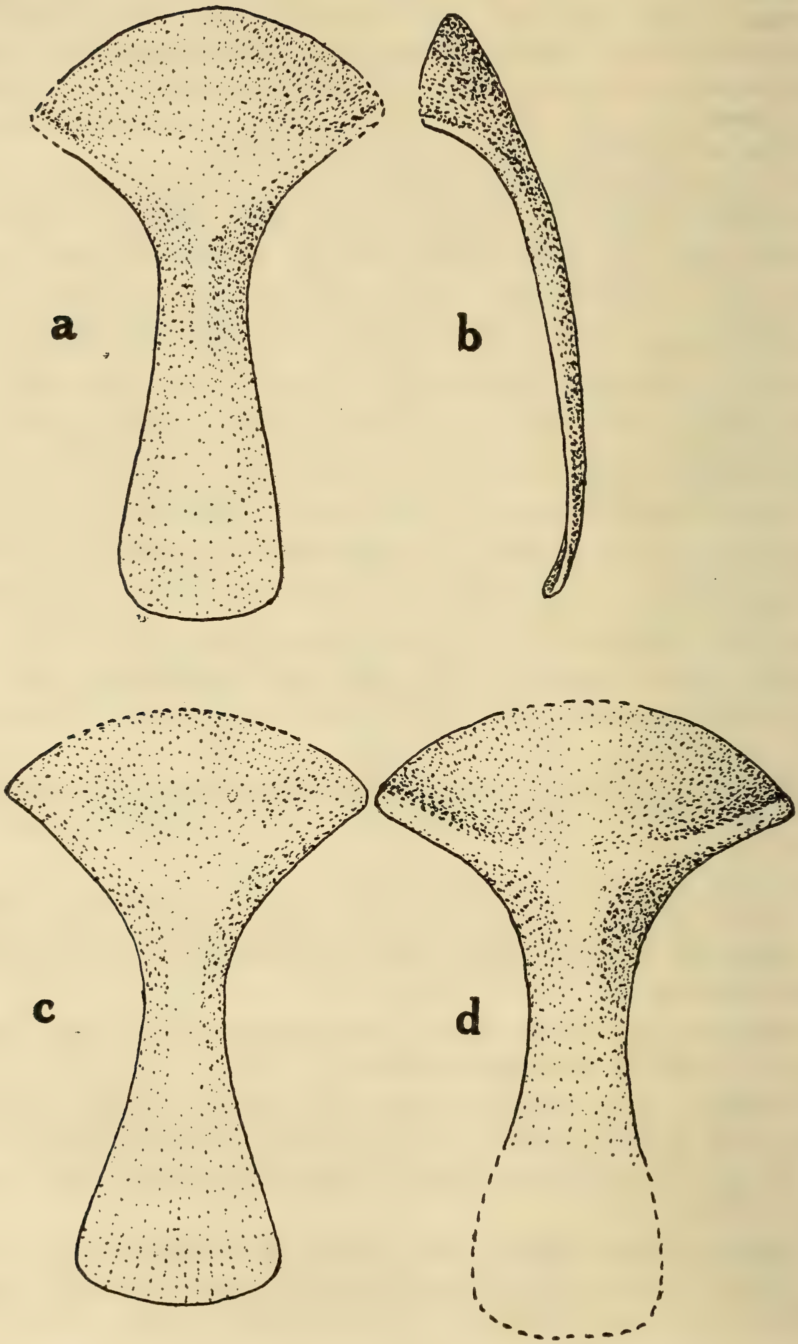
The radius is relatively long (186-204 mm.); it is a slender nearly featureless bone or is fairly robust, with a fairly strong proximo-postaxial flange; the ventral face is longitudinally moderately concave; the proximal facet is slightly convex.

The manus, fully known in only one specimen, has the carpal formula 3-4, 1-2, 5, and the phalangeal formula 2, 3, 3, 3, 3.

The pelvis. As our collection contains only a single incomplete Moschopid ilium of the genus *Avenantia,* I am extracting the characteristic features for this group from the descriptions by Broom (11), Romer (25), Gregory (18) and Byrne (16).

The pubo-ischiadic plate is short (70-80% of the height of the pelvis); the supra-acetabular part of the ilium is high and fairly short (height 73%-75% of its antero-posterior length); the anterior process of the iliac

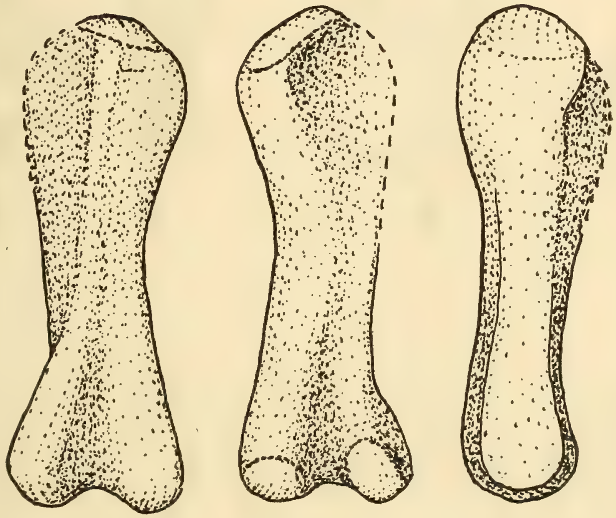
Fig. 41.



Interclaviculae of *Moschops capensis*. (× $\frac{1}{8}$.) a. S.A.M. 11972, in ventral view. b. S.A.M. 11972, in lateral view. c. S.A.M. 11972a, in ventral view. d. S.A.M. 11975, in ventral view.

blade is fairly long and high and diverges fairly strongly laterally; the posterior process is somewhat shorter and appreciably to greatly lower than the anterior process, and its ventro-posterior edge lies fairly horizontally and this is slightly everted, but without forming a definite ridge for the ilio-fibularis; the dorsal iliac edge is slightly folded over laterally; there is apparently no face for the attachment of a rib lying anteriorly of the main sacral rib on the inner face of the anterior iliac process.

Fig. 42.



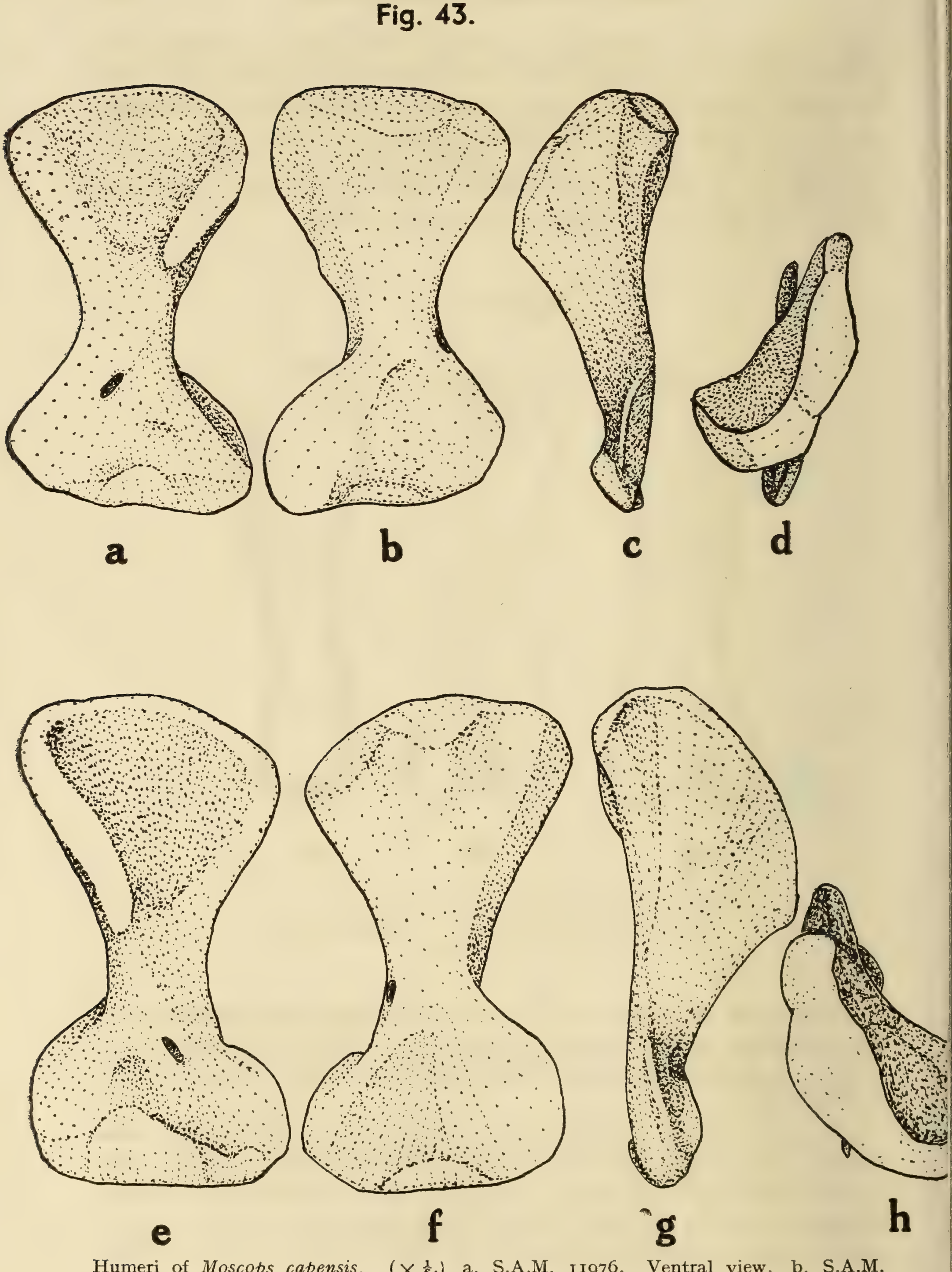
a b c

Femur of *Moschops capensis.* S.A.M. 11974. (× 1/8.) a. Dorsal view. b. Ventral view. c. Anterior view.

In the pubis the anterior edge is everted and ends antero-externally in a low tuberculum pubis; the pubes barely meet in their posterior part in a median symphysis; the two ischia meet below in a deep symphysis forming a median keel.

The femur of the Moschopids is a medium-sized, fairly robust bone (length 310-414 mm.); the width over the external trochanter is fairly small to fairly great (120?-205 mm.); there is no notch separating the external trochanter from the proximal surface; the preaxial face is deeply concave and the caput preaxially directed; the internal trochanter is undeveloped;

Fig. 43.



Humeri of *Moscops capensis*. (× 1/6.) a. S.A.M. 11976. Ventral view. b. S.A.M. 11976. Dorsal view. c. S.A.M. 11976. Anterior view. d. S.A.M. 11976. Proximal view. e. S.A.M. 11975. Ventral view. f. S.A.M. 11975. Dorsal view. g. S.A.M. 11975. Anterior view. h. S.A.M. 11975. Proximal view.

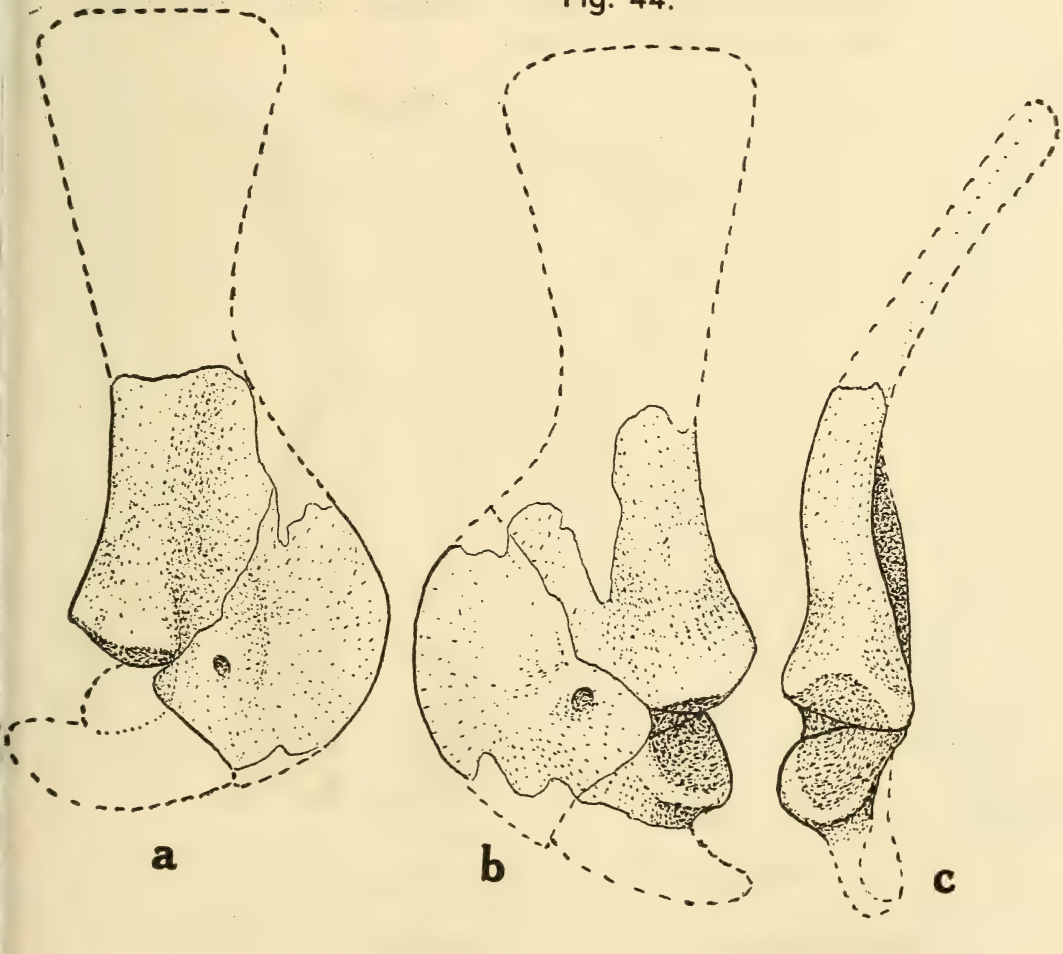
the shaft is fairly long, fairly to moderately broad (84-110 mm.); the condyles are much distally directed, with the external condyle situated slightly or considerably further distally than the internal condyle; the ilio-tibialis ridge is fairly strong and the area for the insertion of the ilio-femoralis quite broad.

The tibia is medium-sized (length 210-270 mm.); cnemial ridge and groove fairly well developed.

The fibula is lightly built, slender and relatively long (222-258 mm.).

The pes is only fully known in one species; here the tarsal formula is 2, 1, 4 and the phalangeal formula 2, 3, 3, 3, 3.

Fig. 44.



Scapulo-coracoids of *Moschops capensis*. ($\times \frac{1}{8}$.) a. S.A.M. 11976a. Lateral view. b. S.A.M. 11976b. Lateral view. c. S.A.M. 11976b. Posterior view.

Genus *Moschops* Broom

The pectoral girdle is lightly built; the scapula is fairly high (440-515 mm.) with the upper part of the blade fairly narrow (174-190 mm.); the glenoidal facet of the scapula faces externally as well as ventro-posteriorly. The femur is a medium-sized fairly robust bone (length 310-390 mm.). For other characters see the family description.

Moschops capensis Broom

The specific description is as for the genus.

Topotypes: A.M.N.H. 5551-5557. Remains of seven or eight skeletons, associated with skulls. Spitskop, Laingsburg. Low? *Tapinocephalus* zone. Coll. Whaits and Broom.

Fig. 45.

Scapulo-coracoid of *Moschops capensis*. (× ⅛.) S.A.M. 11976e. a. Lateral view. b. Posterior view.

Referred specimens in the S.A.M. collection:

S.A.M. 11292. An ulna (Fig. 40c), associated with a skull 11291.

S.A.M. 11971. A distorted humerus, associated with a distorted skull.

S.A.M. 11972. Two interclaviculae (Fig. 41 a-c) and two distal and one proximal end of the clavicle (Fig. 17e), found near a skull, 11972.

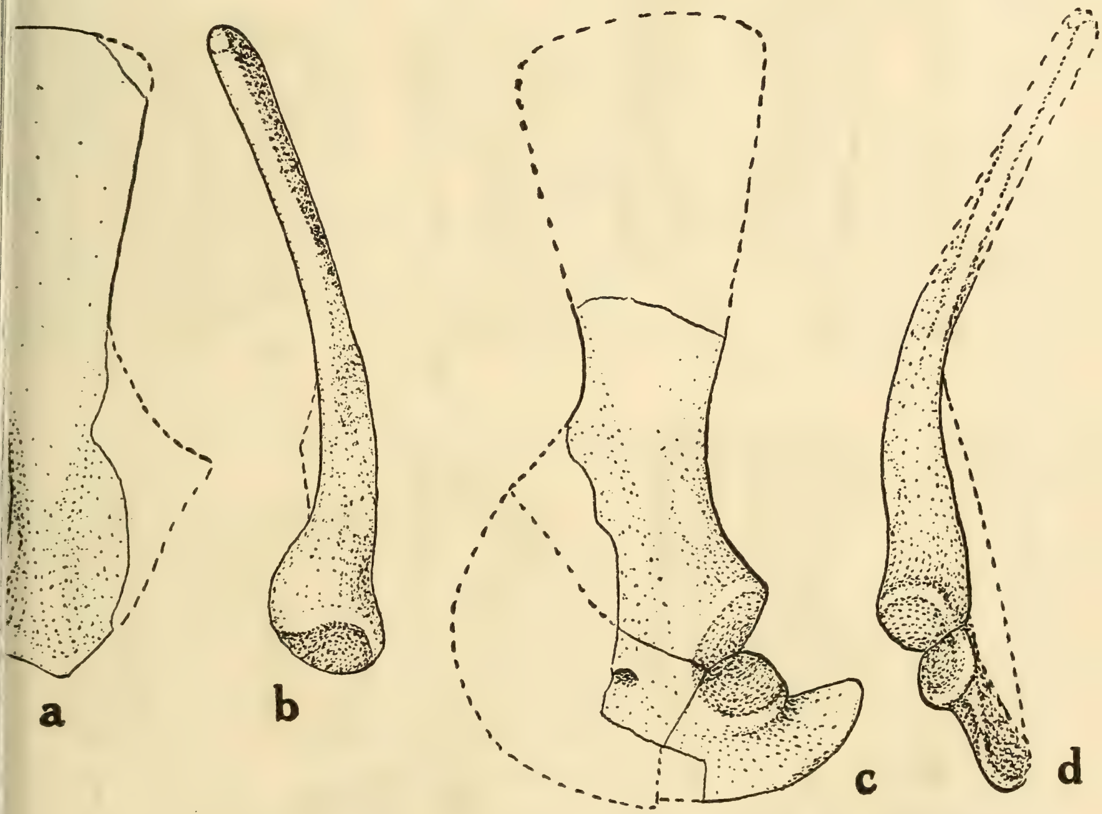
S.A.M. 11974. A femur (Fig. 42), associated with a skull.

S.A.M. 11975. Part of a scapula, a humerus (Fig. 43 e-h) and an incomplete interclavicula (Fig. 41d).

S.A.M. 11976. A good humerus (Fig. 43 a-d).

S.A.M. 11976 a, b, c, d and e Five coraco-scapulae (Figs. 44 and 45).

Fig. 46.

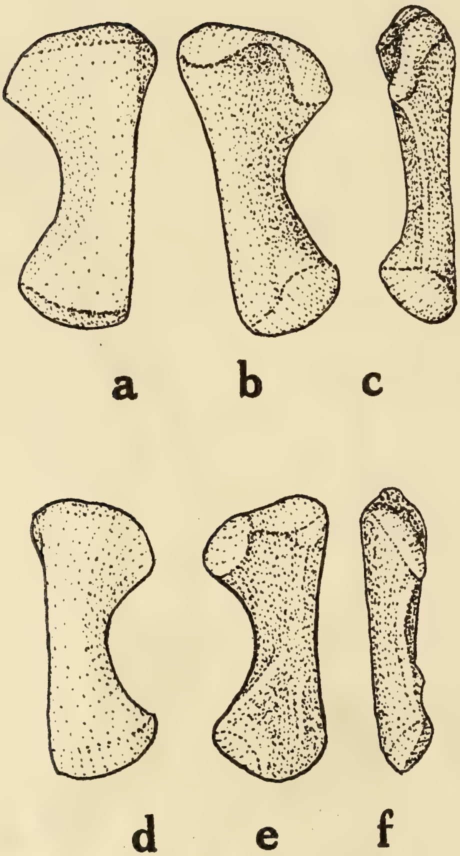


Scapula of *Moschops capensis*. S.A.M. 11977a. ($\times \frac{1}{8}$.) a. Lateral view. b. Posterior view. Coraco-scapula of *Moschops capensis*. S.A.M. 11977b. ($\times \frac{1}{8}$.) c. Lateral view. d. Posterior view.

S.A.M. 11977 a-d. A scapula (Fig. 46a, b) and an incomplete coraco-scapula (Fig. 46c, d), two fibulae (Fig. 47) and three tibiae (Fig. 48), together with a number of incomplete and weathered girdle and limb-bones.

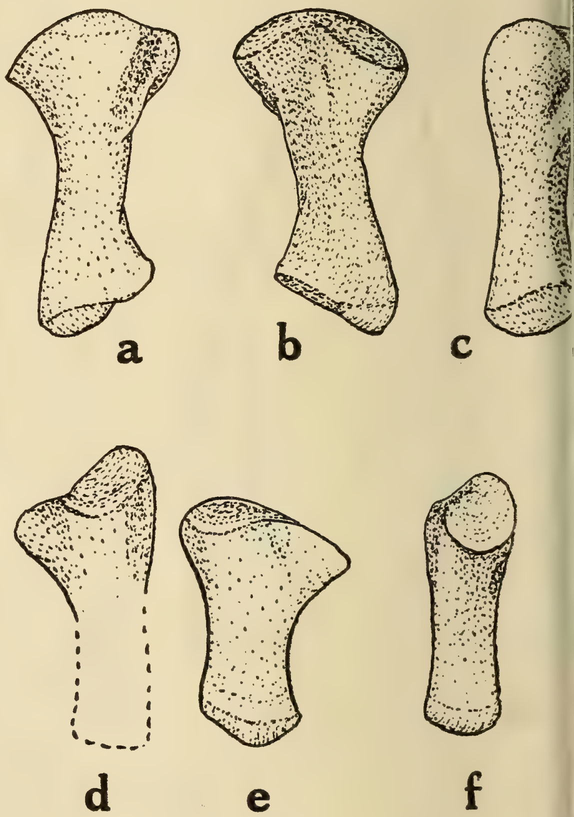
S.A.M. 11978. An isolated coracoid.

Fig. 47.



Fibulae of *Moschops capensis*. (× ⅛.)
a. S.A.M. 11977c. Dorsal view.
b. S.A.M. 11977c. Ventral view.
c. S.A.M. 11977c. Anterior view.
d. S.A.M. 11977d. Dorsal view.
e. S.A.M. 11977d. Ventral view.
f. S.A.M. 11977d. Anterior view.

Fig. 48.

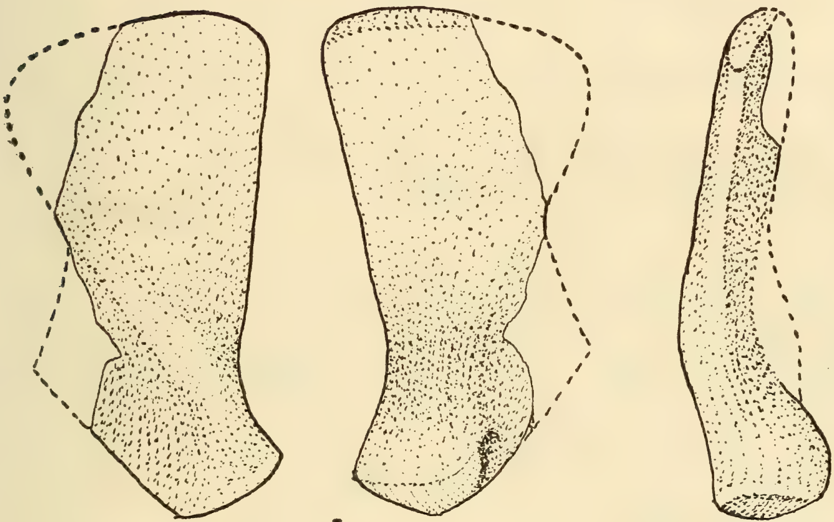


Tibiae of *Moschops capensis*. S.A.M. 11977. (× ⅛. a. Normal left tibia in dorsal view. b. Normal lef tibia in ventral view. c. Normal left tibia ii posterior view. d. Deformed left tibia in dorsa view. e. Crushed right tibia in dorsal view f. Crushed right tibia in posterior view.

All the above specimens were found in an area of about 500 sq. yards, associated with the remains of at least twenty *Moschops* skulls, mostly badly weathered.

Kruisvlei, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

Fig. 49.



a b c

Scapula of *Avenantia kruisvleiensis*. S.A.M. 9167. (× ⅛.) a. Lateral view. b. Internal view. c. Posterior view.

Genus *Avenantia* Boonstra

The girdles and limbs are very inadequately known. The scapula is low (400 mm.), and apparently with a very broad blade (width 210 mm.); the glenoidal facet faces ventro-posteriorly and not externally at all; the supracoracoid canal crosses the suture into the scapula to open into the subscapular groove. The ilium is incompletely preserved, but its blade is fairly low, and both the anterior and posterior processes are long and low.

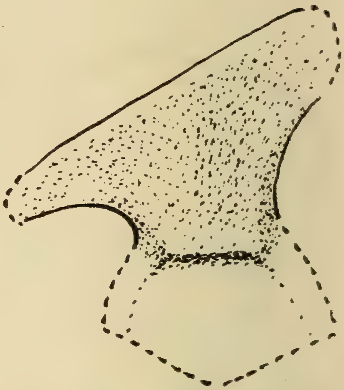
On the other hand the femur is very *Moschops*-like; it is a moderately robust bone with a length of 378 mm.; 168 mm. wide over the external trochanter; the preaxial face is deeply concave and the caput directed well preaxially; the shaft is fairly slender (diams. 96 × 60 mm.); the condyles face ventro-distally and the postaxial condyle is situated much further distally than the preaxial condyle.

Avenantia kruisvleiensis Boonstra

The specific description is as for the genus.

Type: S.A.M. 9167. A scapula, a weathered ilium (Fig. 50) and a good femur (Fig. 51), associated with a fairly good skull. Kruisvlei, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

Fig. 50.

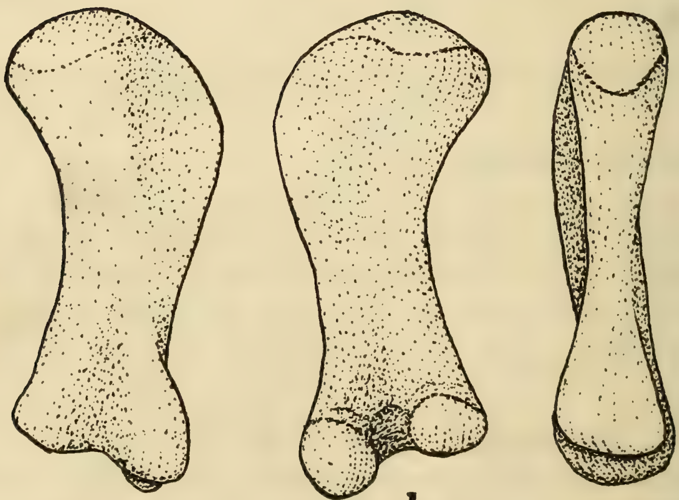


Right ilium of *Avenantia kruisvleiensis*. S.A.M. 9167. (× $\frac{1}{6}$.) Lateral view.

Genus *Moschognathus* Broom

There is no specimen in the South African Museum referable to this genus and in the only known specimen only some features of the pelvis and femur are known. These point to a large measure of similarity with the corresponding bones in *Moschops* (see Gregory's (18) Plate).

Fig. 51.



a b c

Femur of *Avenantia kruisvleiensis*. S.A.M. 9167. (× $\frac{1}{6}$.)
a. Dorsal view. b. Ventral view. c. Anterior view.

Moschognathus whaitsi Broom

Type: A.M.N.H. 5602. Part of the pelvis, two femora and partial vertebral column, associated with parts of a skull and lower jaw. Beaufort West District. ? *Tapinocephalus* zone. Coll. Whaits.

Genus *Pnigalion* Watson

In our collection there is no specimen that can be referred to *Pnigalion*. In the only known specimen in the British Museum, Watson (29) has associated with the skull a humerus, femora and a tibia. The humerus is medium sized and fairly robust (length 455? mm.) with a greatly expanded proximal end (width 246 mm.); the shaft is fairly long and broad (breadth 102 mm.); the strong delto-pectoral crest terminates well proximal of the entepicondylar foramen; the ectepicondyle apparently greatly expanded as a thin sheet of bone.

The femur figured by Watson is a stout and fairly squat bone (length 420 mm.); width over the external trochanter 216 mm. and the width of the shaft 144 mm.). Another femur, consisting of distal and proximal ends not in contact, represents a long fairly slender bone with a preaxially directed head. I took the following measurements in 1934: width across external trochanter 205 mm., across the epicondyles 170 mm. and the diameters of the shaft 110 × 70 mm. It would thus appear that Watson's' figure is that of a dorso-ventrally crushed femur, which thus appears much broader than it was in life and in that case it would not be so very different from the *Moschops* femur.

Pnigalion oweni Watson

The specific description is as for the genus.

Type: B.M. R.3596 (and R.3606). A humerus, femora and tibia, considered to be associated with a partial skull. De Cypher, Beaufort West. Low? *Tapinocephalus* zone. Coll. unknown?

Genus *Moschoides* Byrne

As there is no specimen referable to this genus in this collection I am extracting the following from Byrne's description:

"The scapula is a massive bone, thickened greatly along its posterior edge. It forms the upper part of the glenoid cavity. The coracoid, which forms the remainder of the glenoid, is a rather small element, but bears a

well-developed coracoid process. The precoracoid is much larger, considerably thinner, and is moderately convex. It is thickened only in the glenoidal corner where, also, it is pierced by a large supra-coracoid foramen. The clavicles are moderately expanded elements somewhat constricted in their middle portions. The humerus is a powerfully developed element. There is a strong delto-pectoral crest, a somewhat constricted shaft, and two moderately developed distal condyles. Apparently there is only an entepicondylar foramen.

Both radius and ulna are conspicuously flattened antero-posteriorly. The ulna, the longer bone, carries a strong olecranon process.

The carpus consists of three rather large proximal elements, two central elements, and five rather small distal carpals. The metacarpals are unusually small with the exception of the fifth which is expanded and platelike. The phalangeal formula is 2, 3, 3, 3, 3; the first phalanx in each digit being unusually short.

The pelvic girdle is characterised particularly by the large anterior process of the ilium. The acetabulum is roughly circular in outline.

The femur is a long element and is considerably flattened anteroposteriorly. It bears a well-defined head and two sharply demarked distal condyles. The lesser trochanter is not evident but the great trochanter is well developed.

The tibia is very short. While greatly constricted along its shaft, it flares broadly at either end.

The tarsus is represented by a massive astragalus, an expanded platelike calcaneum, a rather small navicular, and four distal tarsals, the first three of which are quite small. It would seem that a good deal of cartilage must have been present in life to complete the ankle structure.

The metatarsals and the digits are similar in size and shape to the corresponding elements in the forefoot. The distal portion of the hindfoot is much weaker, however, in comparison with the forefoot.''

Moschoides romeri Byrne

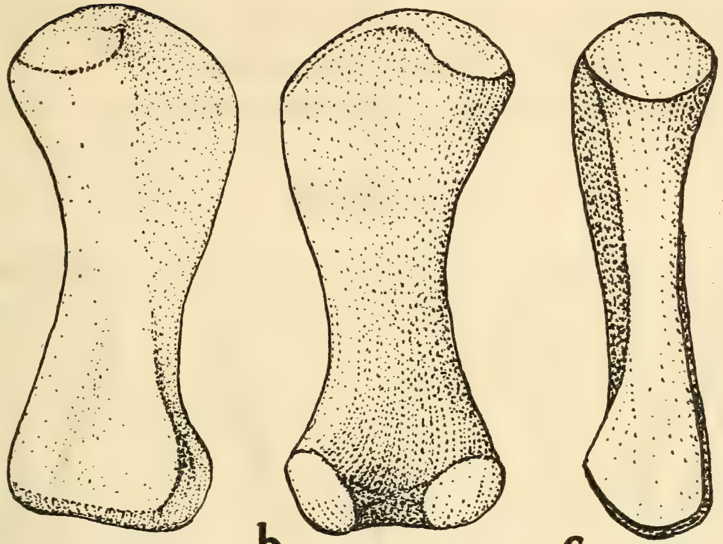
Specific description is as for the genus.

Type: Walker Museum. No. ? The pectoral girdle, humerus, radius, ulna and manus; a fair pelvic girdle, femur, tibia, part of the fibula and the pes. Hottentotsrivier, Beaufort West. High? *Tapinocephalus* zone. Coll. Romer and Miller.

Generically undetermined specimens:

S.A.M. 1057. An isolated good femur (Fig. 52).

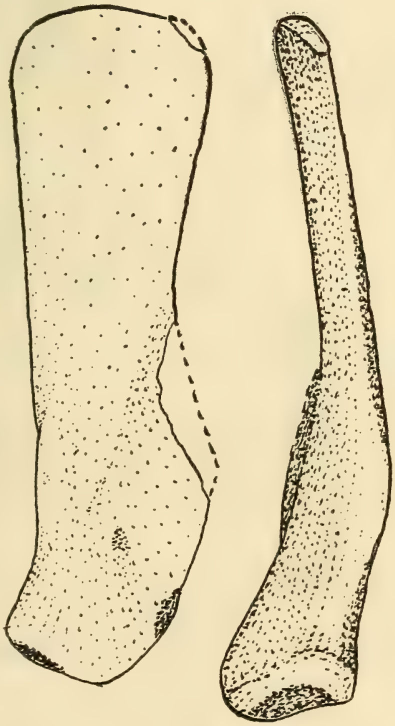
Fig. 52.



a b c

Fig. 53.

Above: Femur of a Moschopid intermediate between *Moschops* and *Pnigalion*. S.A.M. 1057. ($\times \frac{1}{6}$.) a. Dorsal view. b. Ventral view. c. Anterior view.



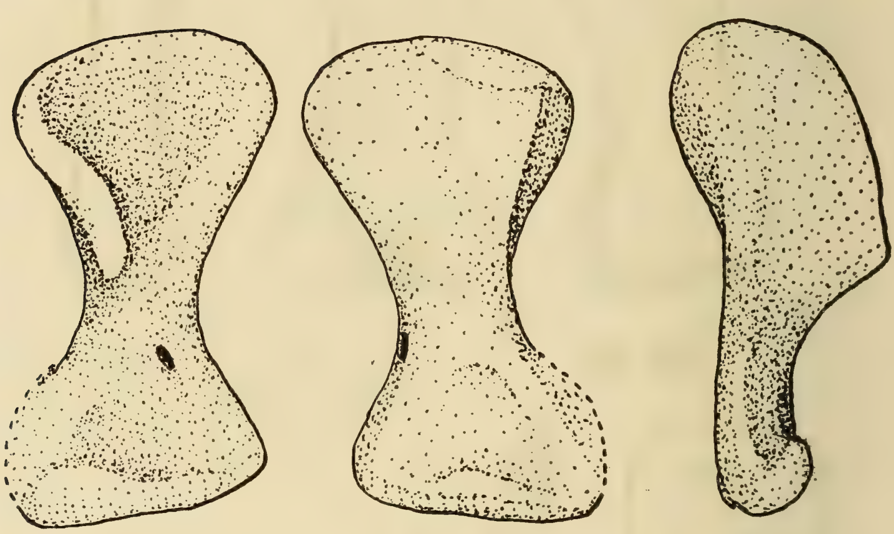
Left: Scapula of a Moschopid. Gen. Indet. S.A.M. 9003. ($\times \frac{1}{6}$.) a. Lateral view. b. Posterior view.

a b

This is a medium sized (length 414 mm.) fairly robust bone (width over the external trochanter 180 mm.); the shaft is fairly long and moderately broad (diams. 102 × 72 mm.); both condyles lie in practically the same plane; the ilio-tibialis ridge is strong. This femur appears to lie about midway between that of *Moschops* and *Pnigalion*.

Letjiesbos, Beaufort West. Mid *Tapinocephalus* zone. Coll. Maddison.

Fig. 54.



a b c

Above: Humerus of ? *Moschops*. S.A.M. 9157. (× $\frac{1}{8}$.) a. Ventral view. b. Dorsal view. c. Anterior view.

Fig. 55.

a b c

Left: Radius of ? *Moschops*. S.A.M. 9157. (× $\frac{1}{8}$.) a. Dorsal view. b. Ventral view. c. Posterior view.

S.A.M. 9003. A good isolated scapula (Fig. 53). This scapula is high (540 mm.) with a fairly narrow blade (width 156 mm.) and with its posterior border fairly straight and the glenoid not facing externally. Klein-Koedoeskop, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

S.A.M. 9101. The distal end of a fibula. Rietfontein, Prince Albert. Low *Tapinocephalus* zone. Coll. Boonstra.

S.A.M. 9124A. A good isolated ulna (Fig. 40 a, a^1). Very similar to the ulna of *Moschops capensis*. Voëlfontein, Prince Albert. Low *Tapinocephalus* zone. Coll. Boonstra.

S.A.M. 9157. A good humerus (Fig. 54), radius (Fig. 55), ulna (Fig. 40 b, b^1) and part of the carpus.

I (4) have recently described the epipodial and the carpus. The humerus is of medium size (length 384 mm.); the proximal expansion is fairly large (210 mm.) and the distal expansion is moderate (212 mm.); the shaft is fairly wide and short (diams. 91 × 66 mm.); although the ulna is very similar to that of *Moschops* the radius is a much more slender bone. This specimen thus lies near *Moschops*.

Wolwefontein, Prince Albert. Low *Tapinocephalus* zone. Coll. Boonstra.

S.A.M. 11581. An isolated flattened femur (Fig. 56). This small femur (length 372 mm.) is most probably of a juvenile *Moschops*. Buffelsvlei, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

S.A.M. 11987. An isolated weathered distal two-thirds of a humerus. The groove on the under surface of the ectepicondyle for the passage of the radial nerve is well developed. Buffelsvlei, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

S.A.M. 11995. An isolated radius (Fig. 57) with a well-developed proximo-postaxial flange. Stouter than S.A.M. 9157. Sutherland District. Low? *Tapinocephalus* zone. Coll. Boonstra.

S.A.M. 3398. An isolated good fibula (Fig. 58). With a length of 252 mm. and its slender build it comes very near that of *Moschops*. Uitkyk, Beaufort West. Low *Tapinocephalus* zone. Coll. Haughton.

Fig. 56.

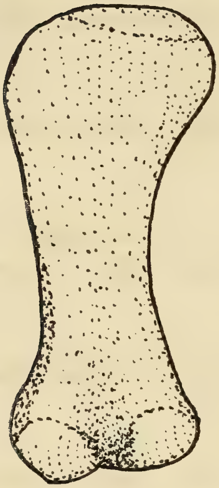


Fig. 57.

a b c

Above: Radius of ? *Moschops*. S.A.M. 11995. ($\times \frac{1}{8}$.) a. Dorsal view. b. Ventral view. c. Posterior view.

Left: Femur of ? *Moschops*. S.A.M. 11581. ($\times \frac{1}{8}$.) Ventral view.

Fig. 58.

a b c

Fibula of ? *Moschops*. S.A.M. 3398. ($\times \frac{1}{8}$.) a. Dorsal view. b. Ventral view. c. Anterior view.

Titanosuchia

Infra-ordinal Characters of the Girdles and Limbs.

The pectoral girdle is large and massive; the scapula is fairly to very high (530-690 mm.) with the upper part of its blade fairly to very broad

(220-426 mm.); the scapular head of the triceps originates from a fairly to very prominent ridge; the internal opening of the foramen suprecoracoideus opens into the deep subscapular groove, i.e. it crosses the suture between the precoracoid and the scapula; the glenoidal facet of the scapula is large, facing ventro-posteriorly and not, or but little, externally. The coracoidal plate is of great antero-posterior extent. The precoracoid is large and strong, with its anterior border thickened, and its greatly thickened dorso-posterior apex forms at most the anterior depressed rim of the glenoid; the foramen supracoracoideus penetrates the bone very obliquely, so that internally it forms a groove in the sutural face crossing to open into the subscapular groove; the outer precoracoidal face is only moderately convex. The coracoid is massive with its large glenoidal facet facing dorso-posteriorly and also much externally.

These three bones have greatly widened sutural faces near the glenoid, but distally from this corner the bones become abruptly thinner along the sutural lines.

The clavicula is a medium-sized to large bone; flat with expanded ends and a constricted waist.

The cleithrum is a strong element with its upper end expanded and projecting beyond the upper scapular border.

The interclavicle is massive to very massive with a greatly widened stem; broadly spatulate anteriorly, and here curving sharply upwards. In some specimens a ridge along the median line on the dorsal surface of the stem limits the movement of the coracoidal plates. A deep groove receives the posterior edge of the lower end of the clavicle.

The humerus is always massive, but varies in size from fairly small, short and squat to very large and long (312-575 mm.); an ectepicondylar foramen is always present; the radial condyle is always strong, thick and well modelled and extends far proximally along the ventral face, in some cases nearly reaching the base of the delto-pectoral crest; the processus medialis lies either nearly in the same plane as the caput or in a more distal plane, i.e. it is proximally or not proximally situated; the processus lateralis is always situated far proximally; the proximal expansion is relatively moderately or very great; the epicondyles are greatly expanded; the shaft is either fairly long or very short, fairly slender or very broad; the ventral opening of the entepicondylar foramen is slitlike or broadly oval; except in one case, the delto-pectoral crest is long; the ectepicondylar foramen is always small and circular.

The ulna is large and massive (length 320-402 mm.).

The radius is large and massive (length 282-318 mm.).

The manus is unknown.

The pelvis has a short pubo-ischiadic plate; the iliac blade is high; the ilio-fibularis ridge is rounded and strong and usually lies vertically; the supra-acetabular buttress is strong with a well-developed notch; the acetabulum faces outwards; the anterior iliac process is moderately to strongly everted; the posterior iliac process is fairly short and high; the iliac blade is concave in antero-posterior direction.

The femur is large and massive (length 498-605 mm.) with the internal trochanter developed as a strong rounded tubercle, situated well away from the preaxial border; the width over the external trochanter, which sometimes has a notch separating it from the proximal face, is great (234-306 mm.).

The tibia is large and massive with strongly expanded ends (length 255-355 mm.).

The fibula is large and stout with a deeply concave anterior face (length 235-345 mm.).

The pes is incompletely known.

Titanosuchidae

Family Characters of the Girdles and Limbs.

The Titanosuchid pectoral girdle is only adequately known in one genus. The pectoral girdle is large and massive; the height is 860-890 mm., and the length of the coracoidal plate is 560-580 mm., which is thus 62-67% of the height. The scapula is high (680 mm.) and the upper end of the blade is broad to very broad (372-426 mm.); the scapular head of the triceps is attached to a sharp ridge or a prominent mound.

The precoracoid is large and massive (340 × 342 mm.).

The coracoid is of medium size but massive (250 × 252 mm.).

The clavicle is a large bone (length 505 mm.); it is medio-laterally flattened, with expanded dorsal and ventral ends, but the waist not greatly constricted; the ventral spatulate end curves inwards to fit over the outer face of the upturned antero-lateral corner of the interclavicle; the dorsal end has its anterior end greatly thickened and is produced dorsally as a short, strong process, which presumably fits into a groove on the lower end of the cleithrum, which is however not preserved.

The interclavicle is a large and massive bone; the length is 570 mm.; width over anterior expansion 455-545 mm.; width over posterior end of stem 215-310 mm. and over the waist of the stem 155-180 mm.; the lateral horns have a thickened postero-lateral edge, anterior to which there is a fairly deep groove to house the ventro-posterior edge of the spatulate end of the clavicle.

The humerus is long and large (length 480-575 mm.); the radial condyle, although strong and extending far along the ventral face, does not reach the plane of the entepicondylar foramen, and lies well distal of the base of the delto-pectoral crest; the processus medialis always lies far proximally — nearly in the same plane as the caput; the proximal expansion is moderately great (240?-310 mm.); the shaft is fairly long and relatively not very broad; the ventral opening of the entepicondylar foramen slitlike or oval.

The ulna has a short massive shaft and a long sigmoid face with a rounded lip.

The radius is a long robust bone.

In the massive pelvis the upper edge of the ilium does not slope strongly downwards in posterior direction; the anterior process is moderately everted; the ilio-fibularis ridge is massive; the ilium forms much the greater part of the acetabulum.

The femur is very large (length 564-605 mm.); the width over the external trochanter is great (275-306 mm.); the preaxial face moderately to deeply concave.

The tibia and fibula large and strong.

Genus *Titanosuchus* Owen

The pectoral girdle poorly known; the coracoid is massive with the glenoidal facet facing much externally.

The humerus is very large (length 530 mm.); the shaft is short and wide (130 mm.); the width over the proximal expansion is 308 mm.; the delto-pectoral crest is fairly short and its extremity is knoblike; the processus medialis is situated well proximally; the capitellum is strong and extends far proximally along the ventral face of the bone; the opening of the entepicondylar foramen ventrally is slitlike; the ectepicondyle is developed as a fairly thin sheet of bone and the foramen is situated well away from the edge of the bone.

The epipodial bones and the manus are unknown.

The pelvic girdle is unknown.

The femur is very long (605 mm.); the width over the external trochanter is 275 mm.; the shaft is fairly narrow (135 mm.); the preaxial face is not very deeply concave, but the caput is preaxially directed.

The fibula is large and massive (295 mm.).

The tibia and pes are not known.

Titanosuchus ferox Owen

The specific diagnosis is as for the genus (see Seeley's (28) plates).

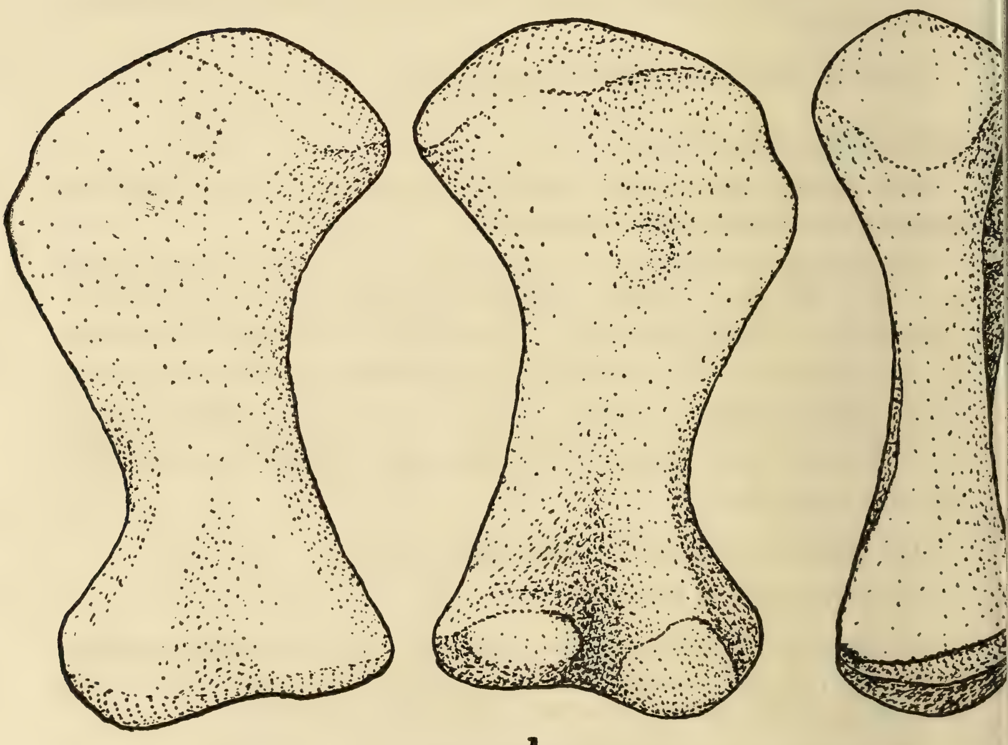
B.M. 49367, coracoid; 49369, humerus; 49368, femur; and 49367b, fibula; all said to be associated with the type cranial material. Koedoeskop, Beaufort West. Mid *Tapinocephalus* zone. Coll. T. Bain.

Referred specimens in the S.A.M. collection:

S.A.M. 739. A fairly good isolated femur, with a length of 570 mm. and shaft diameters of 157 × 65 mm. Beaufort West District. *Tapinocephalus* zone. Coll. Oakley.

S.A.M. 11491. A good isolated right femur (Fig. 59) with a length of 546 mm.; 294 mm. over the external trochanter, which is separated from the proximal face by a distinct notch; the shaft diameters are 144 × 84 mm. Mynhardtskraal, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

Fig. 59.



Femur of *Titanosuchus ferox*. S.A.M. 11491. (× 1/6.) a. Dorsal view. b. Ventral view. c. Anterior view.

Genus *Scapanodon* Broom

All that is known of the pectoral girdle is a single incomplete scapula which shows that the scapular head of the triceps originated from a sharp ridge on the posterior face of the scapula just above the glenoid.

The humerus is fairly long to long (480?-522 mm.); the proximal expansion is not very great (240-264? mm.); the distal expansion fairly great (282-290? mm.); the shaft is fairly short to long and not very broad (diams. 114-118 × 110-121 mm.); the delto-pectoral crest is long with its extremity extending to fairly near the entepicondylar foramen or terminating well proximally of this plane; the caput is oval and fairly massive and lies in nearly the same plane as the processus medialis, which is thus well proximally situated; the twist on the shaft is great (40°); the L.M.L. is strong, forming a pronounced bulge on the dorsal surface of the shaft; the A.D.V.L. is strong and sharp; the entepicondyle is developed as a moderately thick, but not greatly flaring flange of bone, with the foramen ventrally showing a slitlike opening not very far removed from the edge of the bone; the ectepicondyle is a greatly flaring thin sheet of bone pierced vertically by the foramen lying well removed from the edge of the bone.

The epipodial bones of the forelimb and the manus are not known.

The pelvic girdle is massive and high; the pubo-ischiadic plate is short (80% of the height of the pelvis as restored); the supra-acetabular part of the ilium is high and relatively short (the height is 74% of the antero-posterior length); the anterior iliac process, although not fully preserved, appears to have been fairly short, but fairly high, and it is only moderately everted; the posterior iliac process is short and has its posterior edge directed much upwards and this edge is folded over to form a massive ilio-fibularis ridge, which forms a prominent feature on the outer iliac face; anterior to this ridge the iliac blade is deeply concave where the gluteal muscle is attached; the inner face of the anterior process is irregularly pitted for the reception of a rib lying anterior to the main sacral rib; the iliac portion of the acetabulum is very great, forming over two thirds of the acetabulum.

The antero-ventral edge of the pubis is strongly everted with the tuberculum pubis confluent with the strongly thickened outwardly directed antero-ventral edge, which thins as it proceeds towards the median line. The pubic symphysis must have been short and weak. The pubic foramen is a large oval opening.

Only the upper half of the ischium is preserved; it forms only a small part of the acetabulum; its postero-dorsal edge is greatly thickened and it would appear that the ischial symphysis was weak.

The femur is massive and long (564 mm.); its proximal expansion is great, with the width over the external trochanter, which has a notch

separating it from the proximal face, 306 mm.; the preaxial face is fairly strongly concave with the caput moderately thick (134 mm.) and directed moderately preaxially; the shaft is fairly long but very broad (162 mm.); the preaxial condyle is much weaker than the postaxial condyle, which also lies further distally and is very massive (174 mm. thick); the femoro-tibialis ridge is strong, but not strongly bulging on the dorsal surface of the shaft.

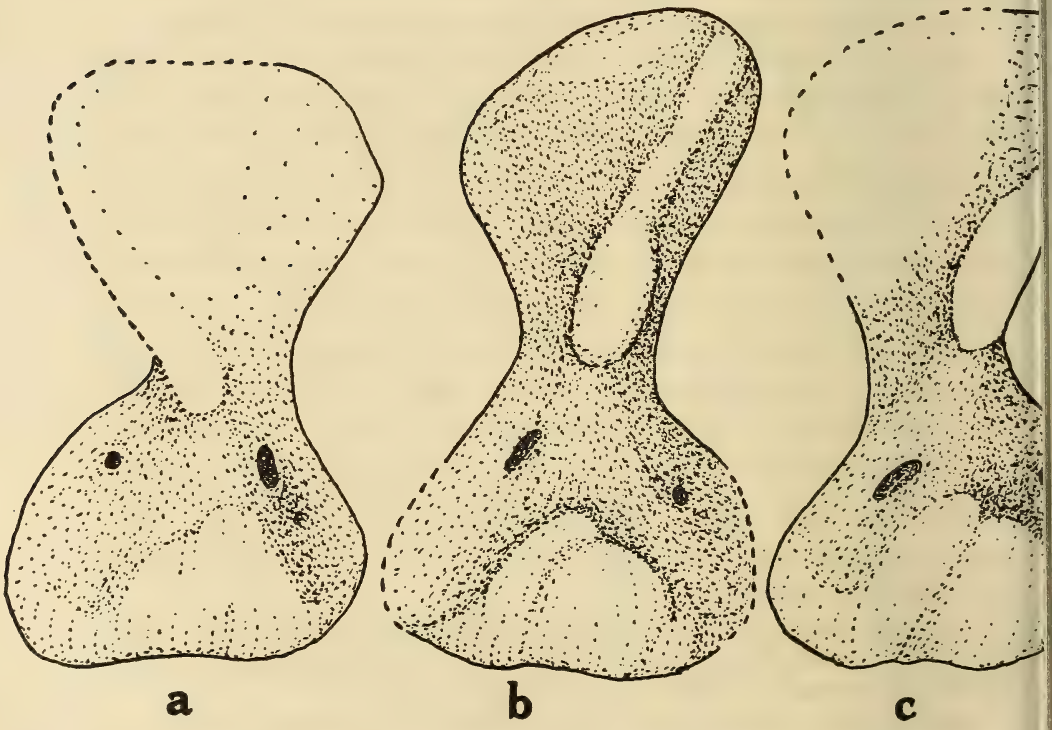
No tibia, fibula or pes is known.

Scapanodon duplessisi Broom

Of the girdle and limb-bones only the humerus is known. The humerus is long (520-522 mm.); the delto-pectoral crest with a swollen end terminates well proximally of the entepicondylar foramen.

S.A.M. 772 and 773. Two fairly good left humeri (Fig. 60 b and c) said to be associated with the poor type jaws. Seekoeigat, Prince Albert. High *Tapinocephalus* zone. Coll. du Plessis.

Fig. 60.



Humeri in ventral view. (× ⅙.) a. *Scapanodon septemfontis*. S.A.M. 5001. b. *Scapanodon duplessisi*. S.A.M. 772. c. *Scapanodon duplessisi*. S.A.M. 773.

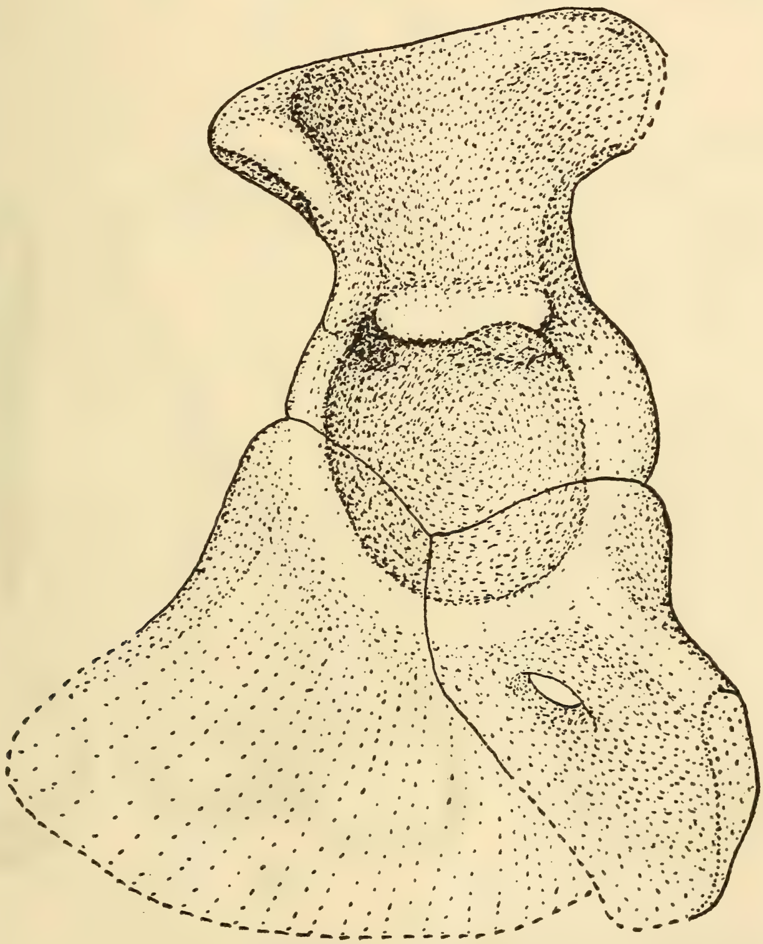
Scapanodon septemfontis Sp. Nov.

I am making the specimen (S.A.M. 5001), which Broom (13) erroneously described as being referable to *Tapinocephalus atherstonei,* the type of a new species of *Scapanodon.*

Nothing is known of the pectoral girdle.

The humerus is large and fairly long (480? mm.); the delto-pectoral crest terminates far distally, but still well away from the ventral opening of the entepicondylar foramen.

Fig. 61.



Pelvis of *Scapanodon septemfontis.* S.A.M. 5001. (× ⅙.) Lateral view.

The rest of the forelimb is unknown.

The pelvis and femur are as described in the generic diagnosis.

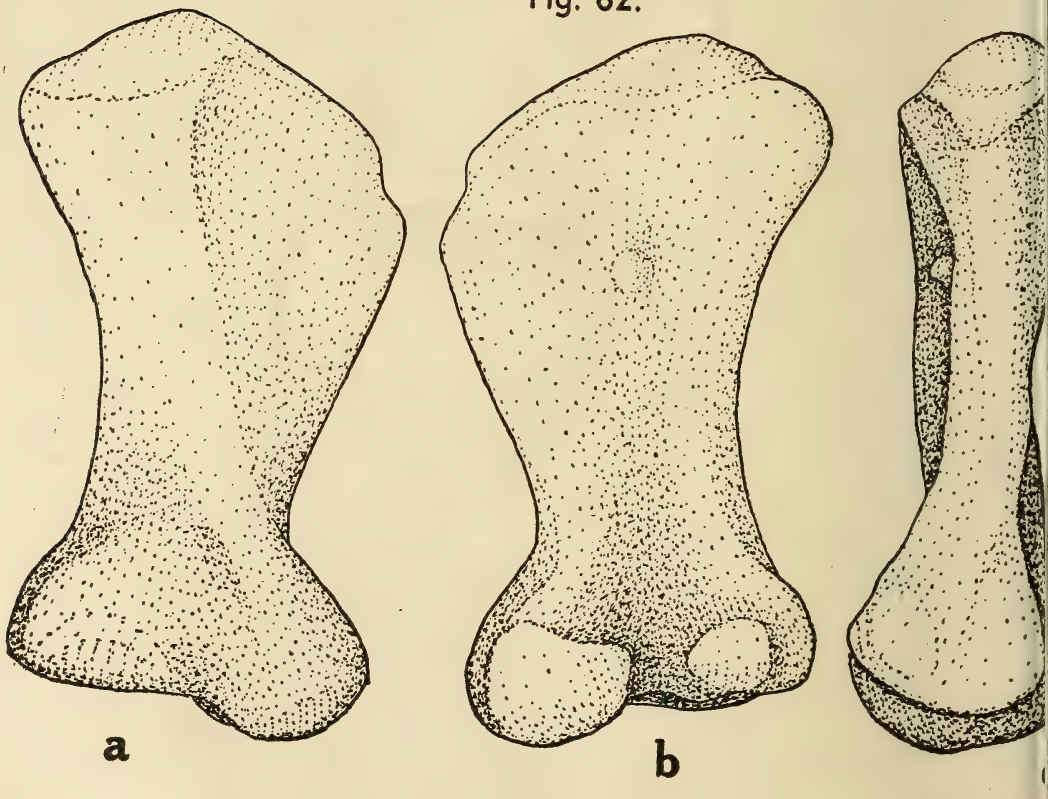
Type: S.A.M. 5001. An incomplete humerus (Fig. 60a), a nearly complete pelvis (Fig. 61) and a good femur (Fig. 62). Sewefontein, Prince Albert. Low *Tapinocephalus* zone. Coll. Haughton.

Referred specimens in the S.A.M. collection:

S.A.M. 1203. A pubis. Letjiesbos, Beaufort West. Mid *Tapinocephalus* zone. Coll. Maddison.

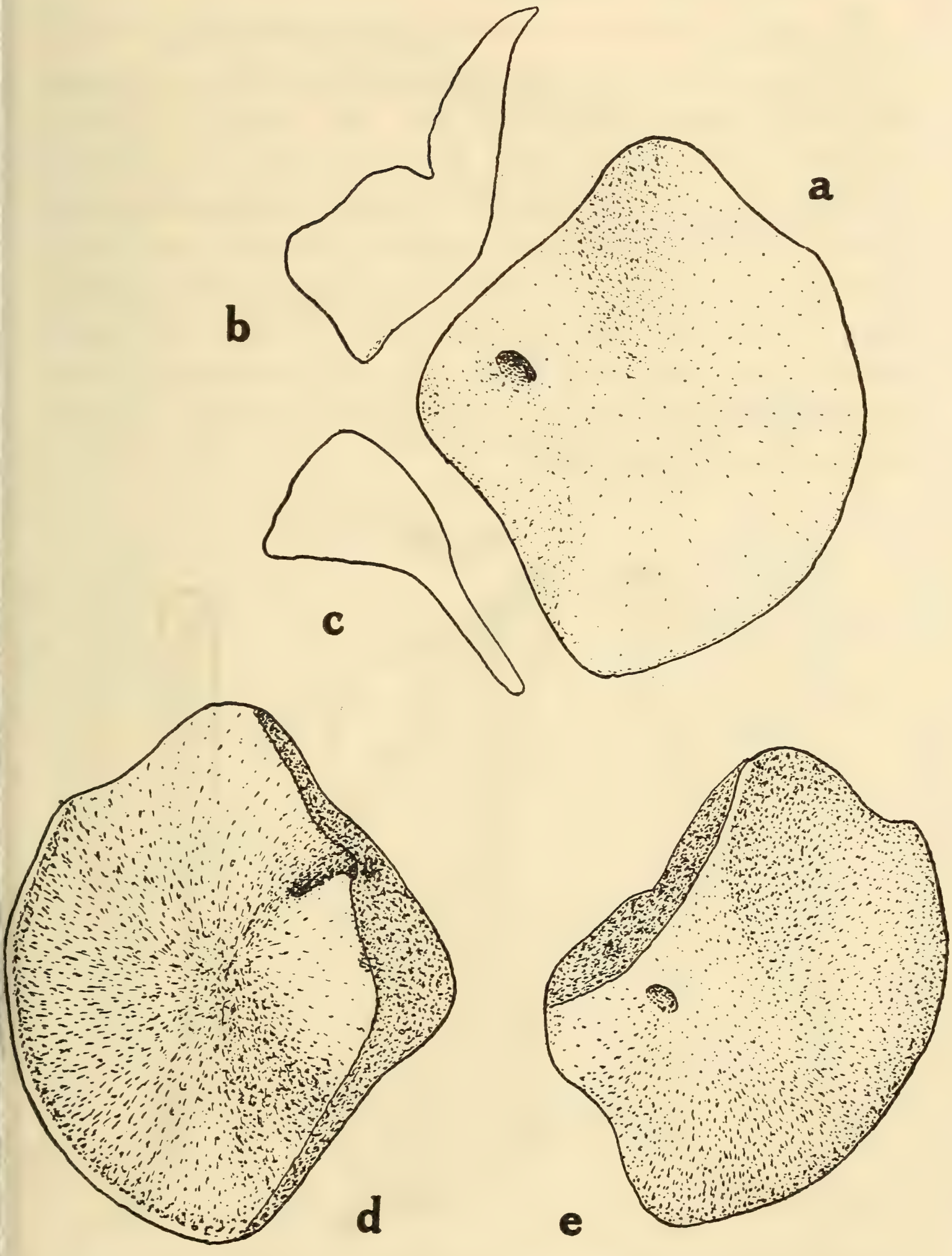
S.A.M. 11578. Part of a scapula and the major part of a humerus. Aasvoëlbos, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

Fig. 62.



Femur of *Scapanodon septemfontis*. S.A.M. 5001. (× ⅙.) a. Dorsal view. b. Ventral view. c. Anterior view.

Fig. 63.



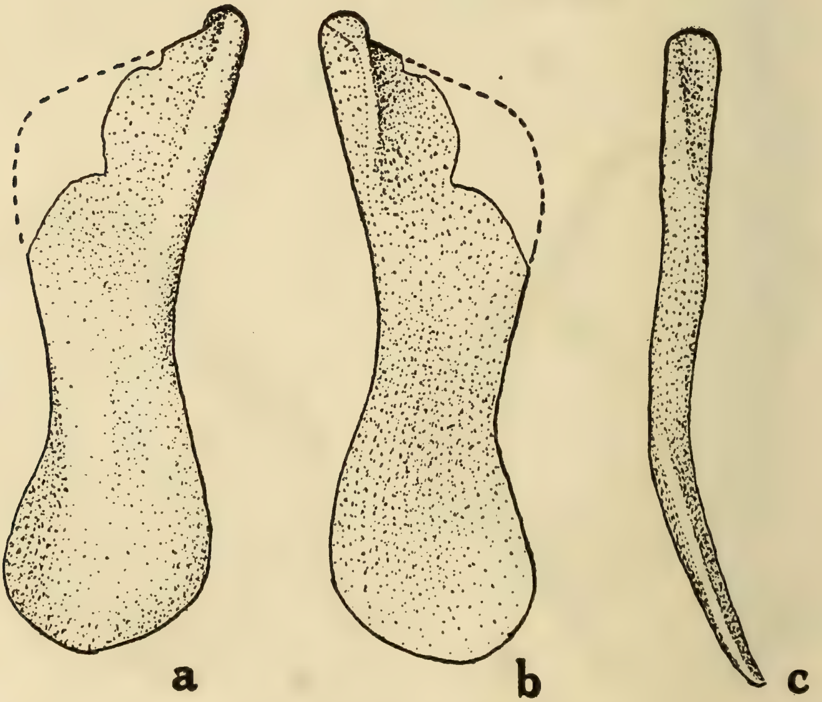
Precoracoid of *Parascapanodon avifontis*. S.A.M. 9127. $(\times \frac{1}{6}.)$ a. Outer view. b. Outline of sutural face for the scapula. c. Outline of sutural face for the coracoid. d. Inner view. e. Lateral view (as projected on to the median plane).

Genus *Parascapanodon* Gen. Nov.

The generic characters of the pectoral girdle are as described for the family.

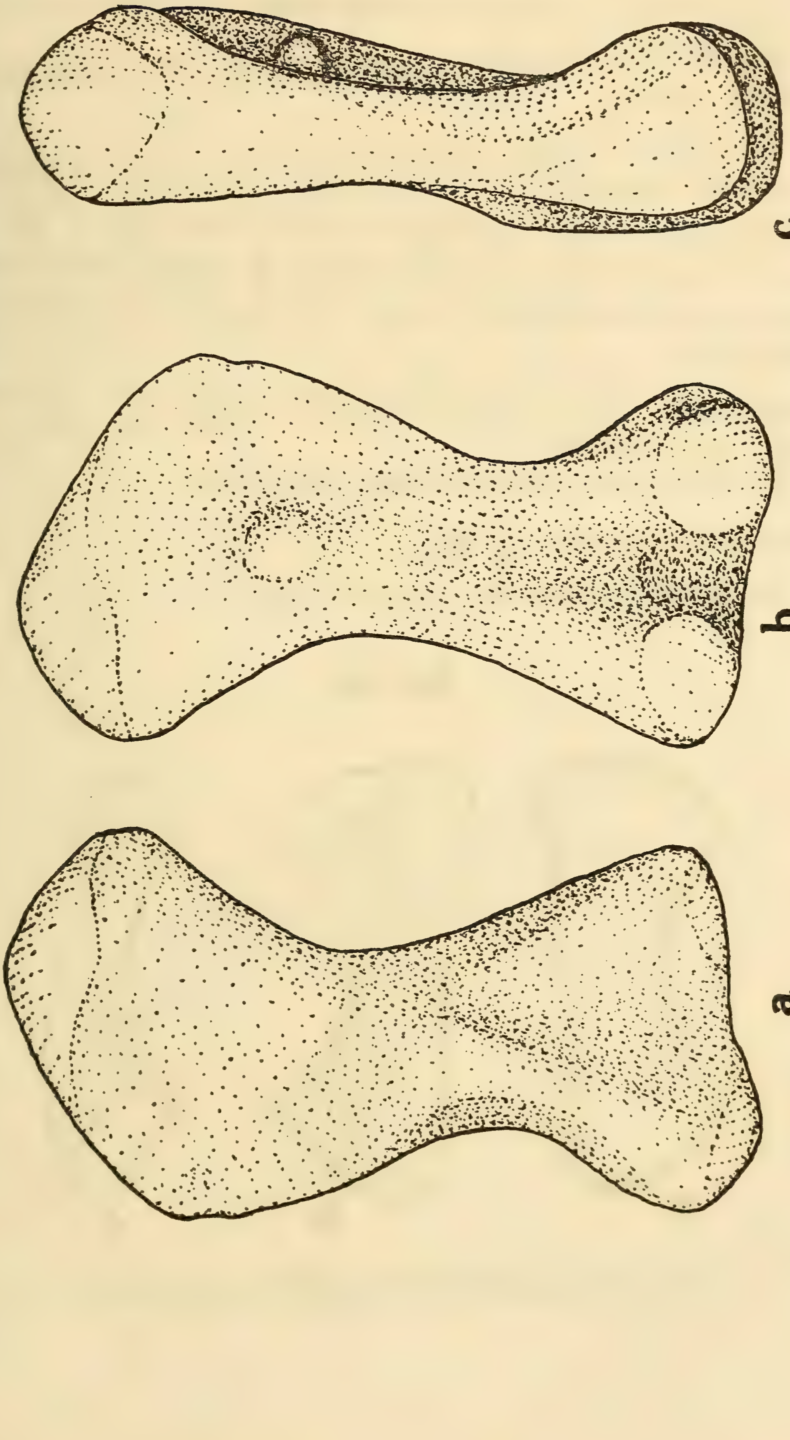
The humerus is very large and massive; the length is 575 mm. and the ends greatly expanded (proximal 310? mm., distal 312 mm.); the shaft is fairly long but very robust (diams. 144 × 142 mm.); the delto-pectoral crest is long, but terminates well proximal of the plane in which the ent-epicondylar foramen lies; the caput is very massive, but short; the processus medialis lies just a little distally of the plane in which the caput lies; the capitellum is very strong and massive and extends far along the ventral face, but does not reach the plane of the entepicondylar foramen; the "twist" on the shaft is large (40°); the L.M.L. is strong, with a massive swelling on the dorsal surface of the shaft; both epicondyles are strongly developed; the ventral opening of the entepicondylar foramen is large and broadly oval, and the ectepicondylar foramen is small and situated well away from the edge of the bone.

Fig. 64.



Right clavicle of *Parascapanodon avifontis*. S.A.M. 9127. (× ⅛.) a. Outer view. b. Inner view. c. Anterior view.

Fig. 65.



Femur of *Parascapanodon avifontis*. S.A.M. 9127. (× $\frac{1}{8}$.) a. Dorsal view. b. Ventral view. c. Anterior view.

The ulna is a large and massive bone (length 372 mm., width over the coronoid process is 200 mm.); the sigmoid face is long, with its ventral part broadly rounded; the coronoid process is situated far distally and the shaft is massive, broad and short.

The radius is a long robust bone (length 294 mm.) with a strong proximo-postaxial flange.

No pelvis is known.

The femur is very long and massive (length 595 mm.); very broad over the external trochanter (300 mm.); the preaxial face is deeply concave, with the caput much preaxially directed and massive (diams. 215 × 167 mm.); the external trochanter is indistinctly separated by a notch from the proximal face; the shaft is fairly long and broad (breadth 150 mm.); wide over the massive distal facets; the area of origin of the femoro-tibialis forms a strong bulging ridge.

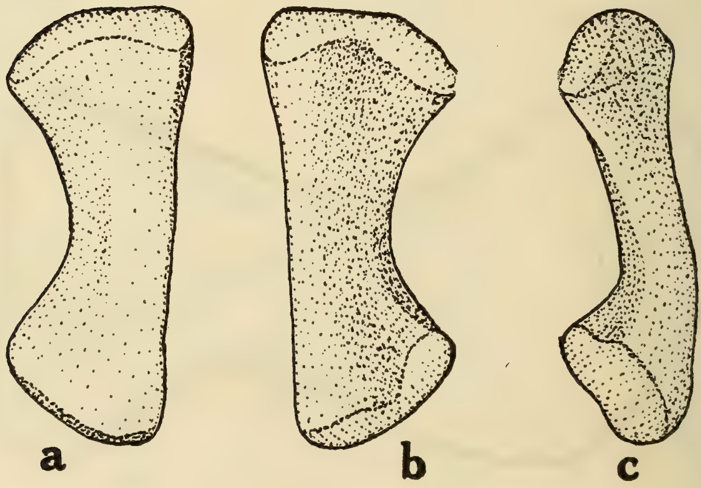
The tibia is large and massive (length 330-355 mm.); the cnemial eminence very massive, continued distally as a strong ridge, with a deep groove lying postaxially.

The fibula is large and stout (length 330-345 mm.).

Parascapanodon avifontis Sp. Nov.

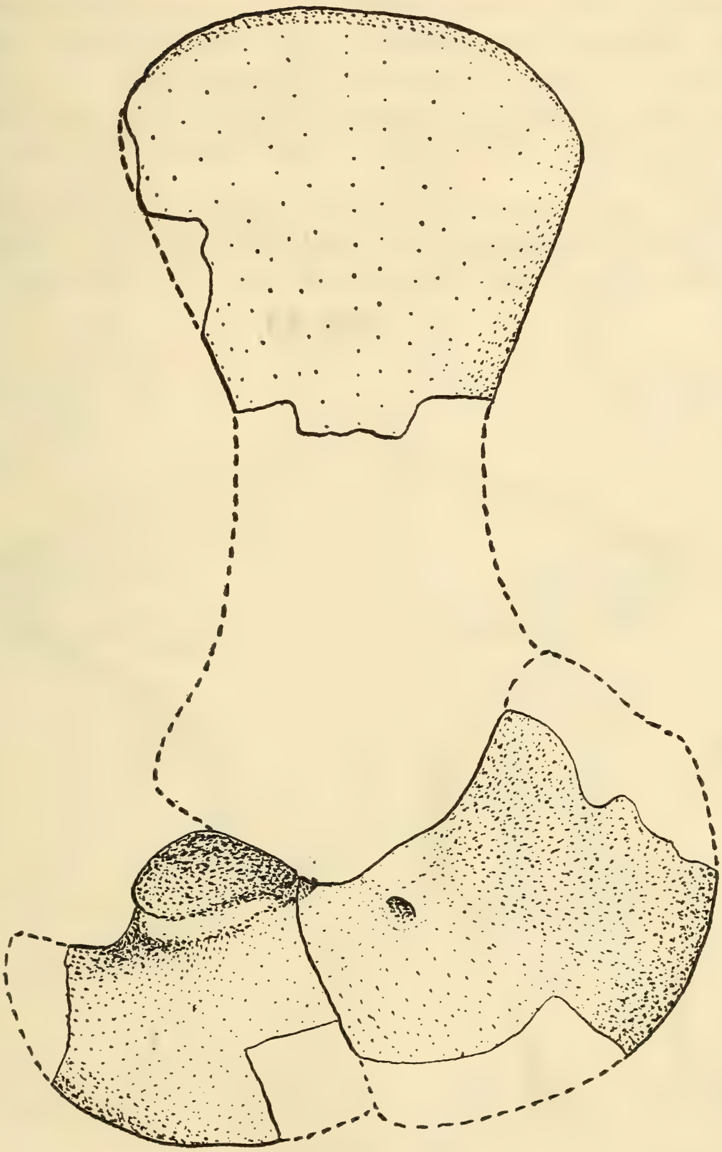
The specific characters are as for the genus.

Fig. 66.



Left fibula of *Parascapanodon avifontis*. S.A.M. 9127. (× ⅛.) a. Dorsal view. b. Ventral view. c. Anterior view.

Fig. 67.



Scapulo-coracoid of *Parascapanodon avifontis*. S.A.M. 9106. (× 1/6.)
Lateral view.

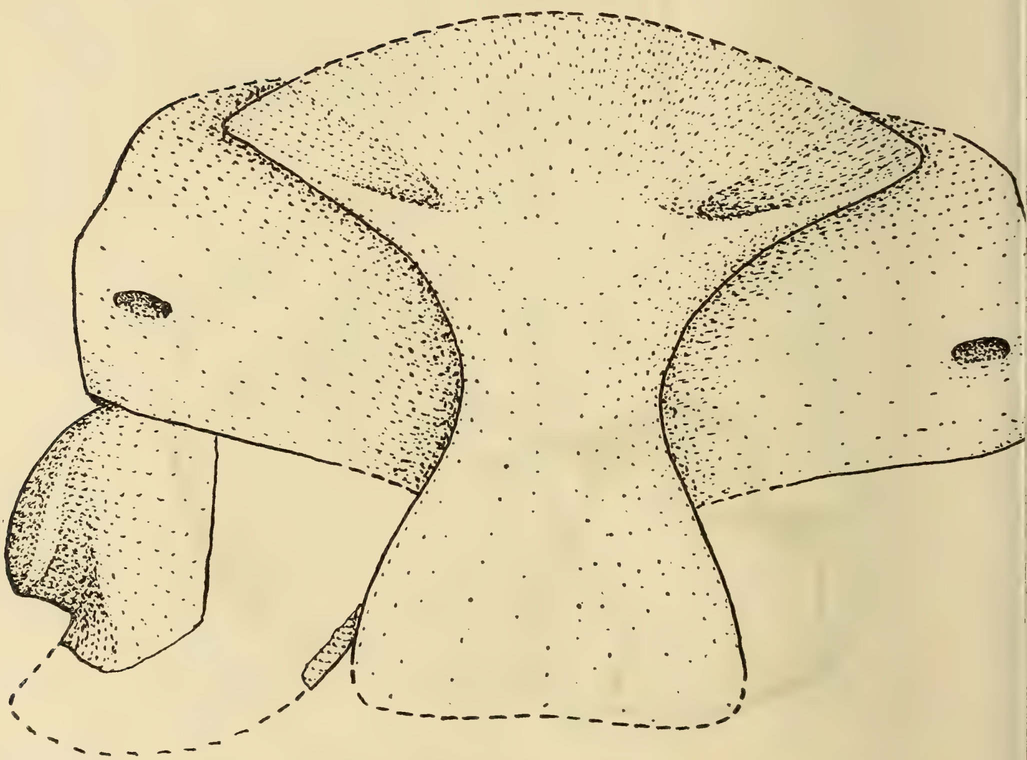
Type: S.A.M. 9127. A very good precoracoid (Fig. 63), a good clavicle (Fig. 64), a good femur (Fig. 65), a well-preserved fibula (Fig. 66), associated with parts of a large skull. Voëlfontein, Prince Albert. Low *Tapinocephalus* zone. Coll. Boonstra.

Paratypes: Although lacking cranial parts, and direct comparison with the type skull parts thus impossible, I have used the following specimens in drawing up the generic description of *Parascapanodon:*

S.A.M. 9106. Parts of the scapula, coracoid and precoracoid (Fig. 67). Veldmansrivier, Prince Albert. Low *Tapinocephalus* zone. Coll. Boonstra.

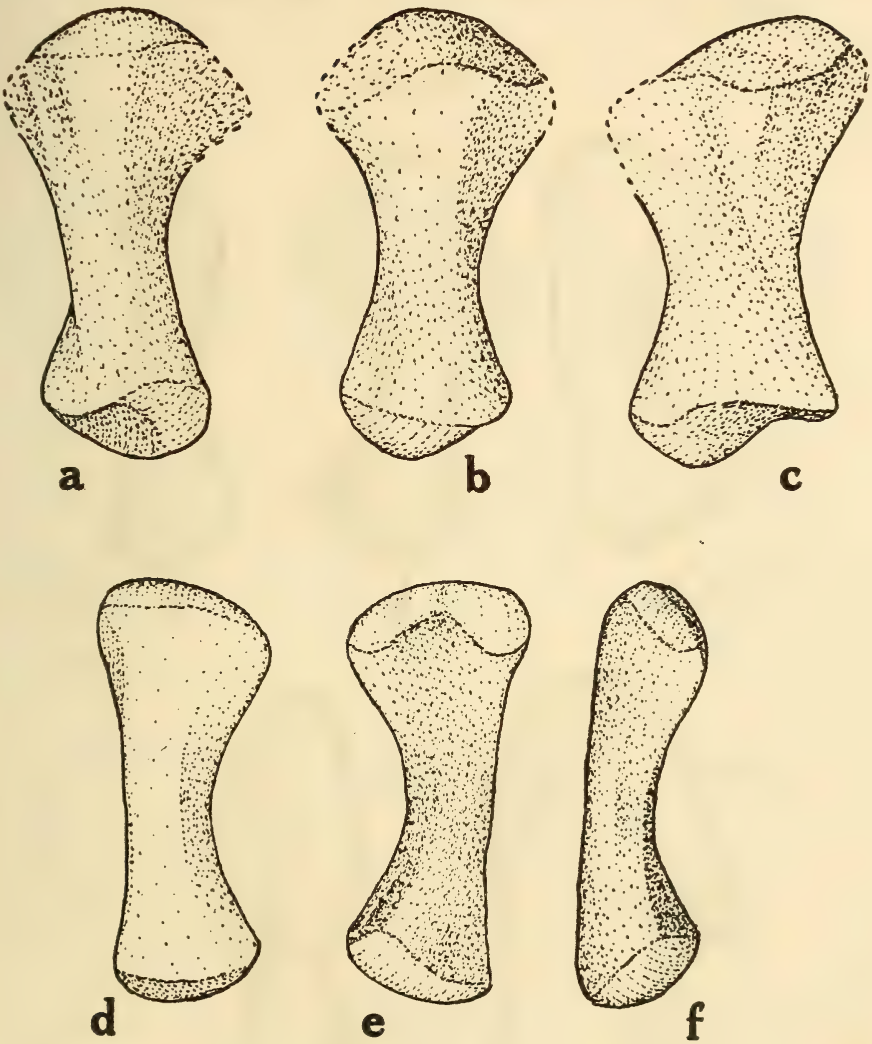
S.A.M. 11488. Parts of the precoracoid, coracoid and interclavicle (Fig. 68) and a tibia (Fig. 69 a-c) and fibula (Fig. 69 d-f). Voëlfontein, Prince Albert. Low *Tapinocephalus* zone. Coll. Boonstra.

Fig. 68.



Interclavicle, precoracoid and coracoid of *Parascapanodon avifontis* in ventral view. S.A.M. 11488. (× ⅛.)

Fig. 69.



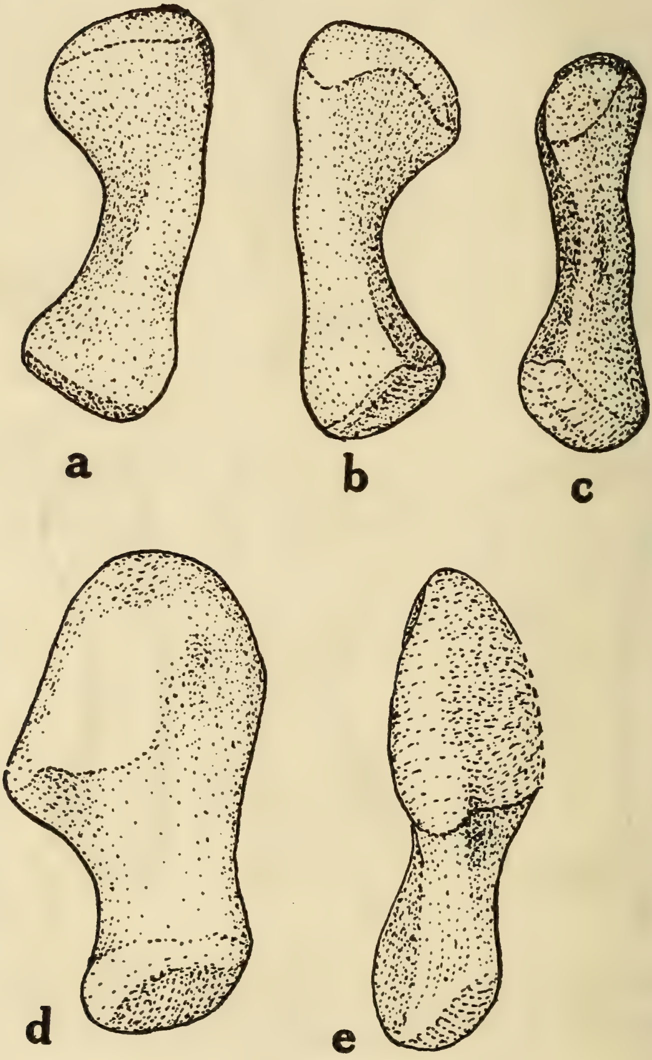
Parascapanodon avifontis. S.A.M. 11488. ($\times \frac{1}{6}$.) a. Right tibia in dorsal view. b. Right tibia in ventral view. c. Right tibia in posterior view. d. Right fibula in dorsal view. e. Right fibula in ventral view. f. Right fibula in anterior view.

These two specimens are included in this species on the ground of the great similarity of their precoracoids to that of the type.

On the similarity of its fibula to that of the type I have also included:

S.A.M. 9163. A good fibula (Fig. 70 a-c) and a fair ulna (Fig. 70 d-e). Wakkerstroom, Prince Albert. Low *Tapinocephalus* zone. Coll. Boonstra.

Fig. 70.

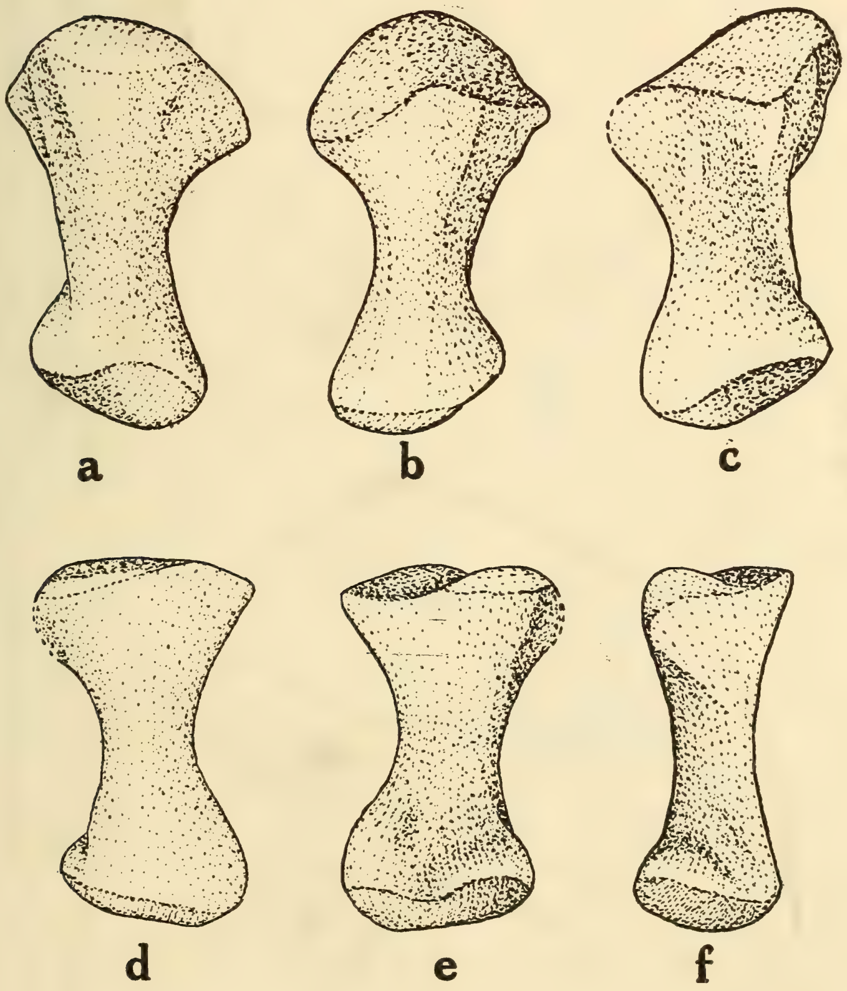


Parascapanodon avifontis. S.A.M. 9163. (× 1/6.) a. Left fibula in dorsal view. b. Left fibula in ventral view. c. Left fibula in anterior view. d. Left ulna in dorsal view. e. Left ulna in anterior view.

On the similarity of its tibia to that of S.A.M. 11488 I have also included:

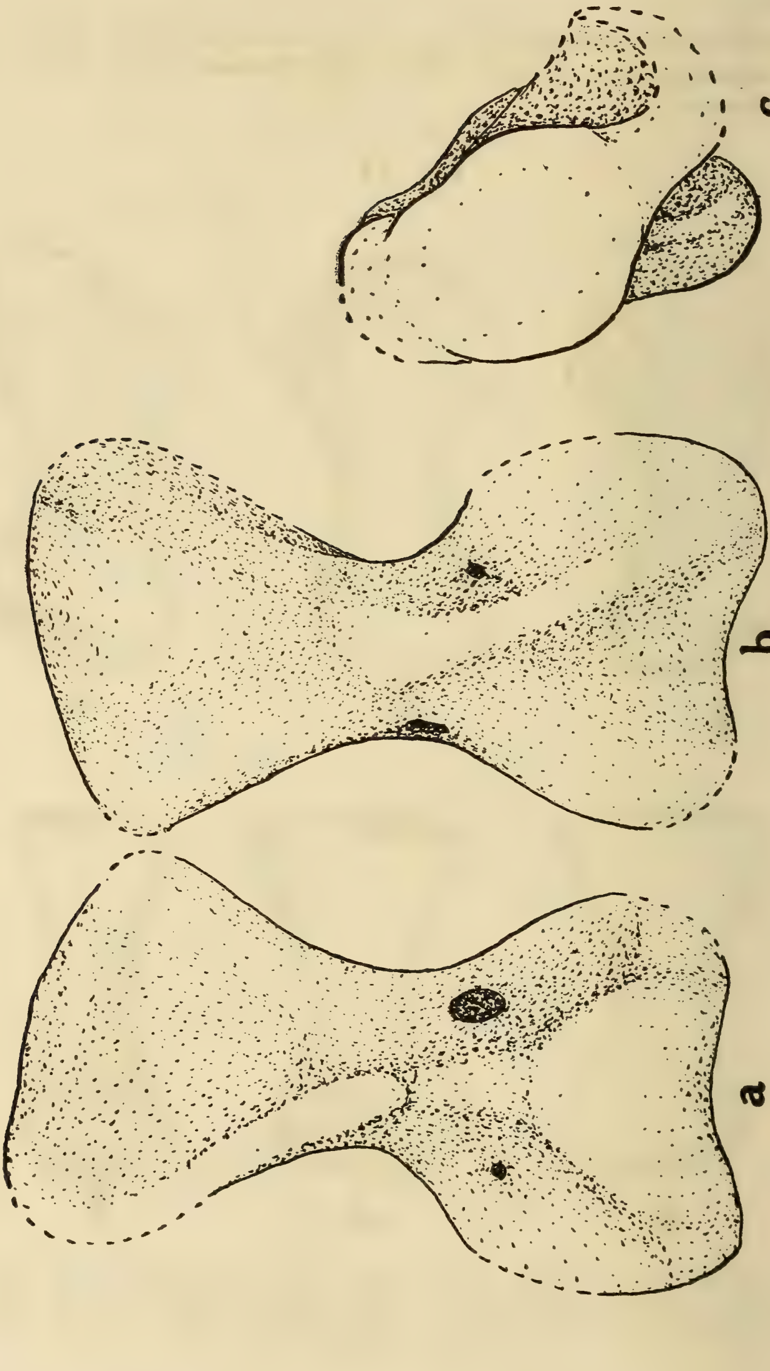
S.A.M. 11299. A good tibia (Fig. 71 a-c) and a good radius (Fig. 71 d-f). Boesmansrivier, Beaufort West. Mid *Tapinocephalus* zone. Coll. Boonstra.

Fig. 71.



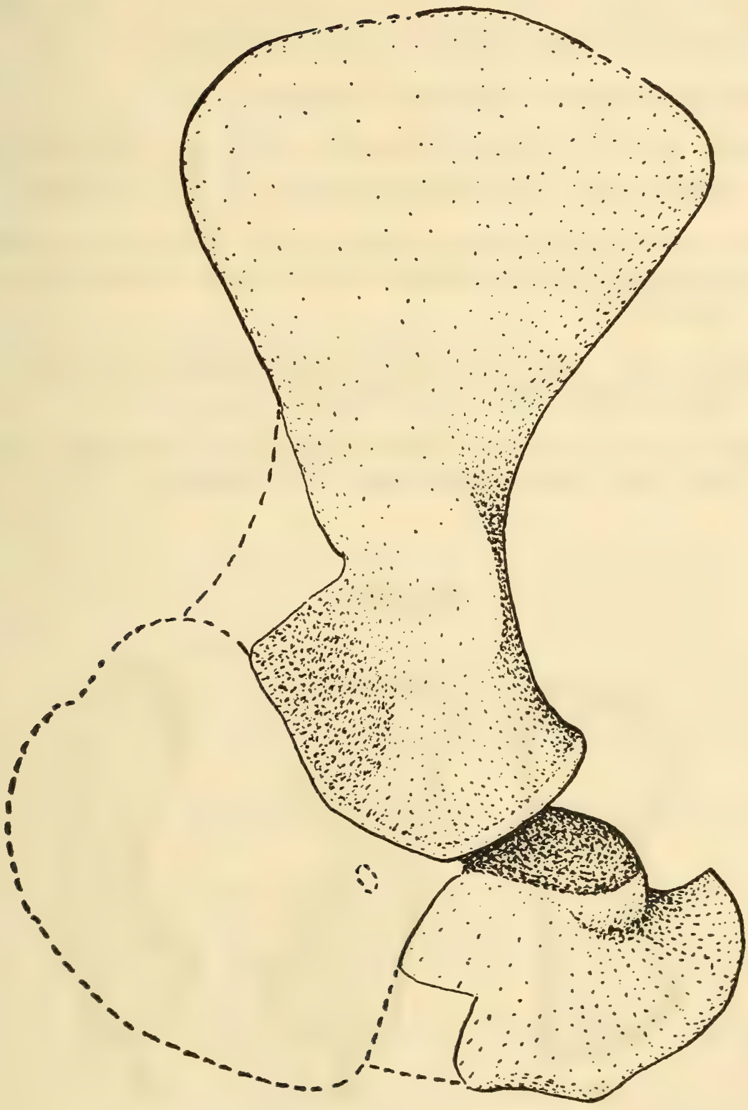
Parascapanodon avifontis. S.A.M. 11299. ($\times \frac{1}{6}$.) a. Right tibia in dorsal view. b. Right tibia in ventral view. c. Right tibia in posterior view. d. Right radius in dorsal view. e. Right radius in ventral view. f. Right radius in posterior view.

Fig. 72.



Humerus of *Parascapanodon avifontis*. S.A.M. 11881. (× 1/6.) a. Ventral view. b. Dorsal view. c. Proximal view.

Fig. 73.



Scapulo-coracoid of *Parascapanodon*. S.A.M. 9010. (× $\frac{1}{8}$.)
Lateral view.

I am including the following isolated humerus as a paratype:

S.A.M. 11881. A fairly good isolated humerus (Fig. 72). Bloukrans, Prince Albert. Mid *Tapinocephalus* zone. Coll. Boonstra.

This very large and massive humerus can only be associated with such a large skull and massive femur as that of *Parascapanodon*.

Referred specimens in the S.A.M. collection:

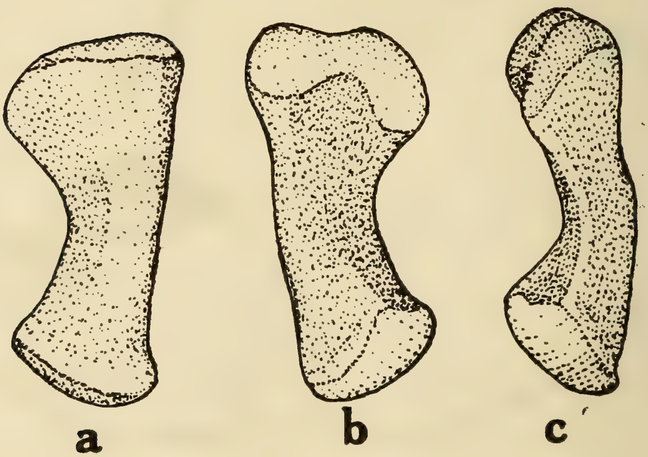
S.A.M. 9010. A scapula and coracoid (Fig. 73). Klein-Koedoeskop, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

The coracoid in this specimen agrees very well with that of the paratype S.A.M. 9106 and I am thus referring it to this genus although it has a much wider scapular blade.

S.A.M. 11938. An isolated tibia. Steenboksfontein, Laingsburg. Low *Tapinocephalus* zone. Coll. Boonstra.

S.A.M. 11989. An isolated good fibula (Fig. 74). Koedoeskop, Beaufort West. Mid *Tapinocephalus* zone. Coll. Boonstra.

Fig. 74.



Fibula of *Parascapanodon*. S.A.M. 11989.
($\times \frac{1}{6}$.) a. Dorsal view. b. Ventral view.
c. Anterior view.

Jonkeridae

Family Characters of the Girdles and Limbs.

The pectoral girdle is large and massive; the height is 650-780 mm. and the length of the coracoidal plate is 385-534 mm., which is thus 59-68% of the height. The scapula is fairly high to high (530-665 mm.) and the upper end of the blade is fairly broad (220-360 mm.); the scapular head of the triceps is attached to a low or a prominent mound.

The precoracoid is fairly large, but not very massive (315-330 × 235-270 mm.).

The coracoid is small to medium-sized, but massive (180-200 × 220-282 mm.).

The clavicle is a large bone (420?-520? mm.) with a greatly constricted waist.

The cleithrum is strong (length 450? mm.).

The interclavicle is a large and massive bone; the length is 396-558 mm.; width over anterior expansion 292-456 mm.; width over posterior end of the stem 210-252 mm. and over the waist of the stem 96-180 mm.; the lateral horns with thickened postero-lateral edge and a deep groove to receive the clavicle.

The humerus is relatively short and small to fairly large (length 312-510 mm.); the capitellum is very strong and extends far along the ventral face to reach the plane of the entepicondylar foramen, and sometimes even the base of the delto-pectoral crest; the processus medialis always lies well distally — in a plane well distal of that of the caput; the proximal expansion is relatively great (222-366 mm.); the shaft is short and broad to very broad (breadth 84-168 mm.); the ventral opening of the entepicondylar foramen is large and oval.

The ulna has a long, fairly massive shaft, and the radius is a long robust bone.

In the pelvis the upper edge of the ilium slopes strongly downwards in posterior direction; the anterior process is strongly everted; the ilio-fibularis ridge is fairly light to moderately massive; the ilium does not form the greater part of the acetabulum.

The femur is not large (length 504 mm.); the width over the external trochanter fairly large (264 mm.).

The tibia and fibula fairly large but fairly slender.

Genus *Jonkeria* van Hoepen

The generic characters are as for the family.

Jonkeria truculenta van Hoepen

In our collection there are no specimens of this species with elements of the girdles and limbs preserved. The following specific characterisation is thus drawn from Broom's (14) account.

Scapula fairly high (530 mm.) and the blade fairly wide (220 mm.); the glenoidal facet faces somewhat externally. The precoracoid just enters the glenoid; it is high (315 mm.) and fairly long (235 mm.); the anterior edge is thin. The coracoid is 200 mm. high and 220? mm. long. The cleithrum is, according to Broom, small and probably fairly similar to that of *Moschops*. Length of clavicle ± 520 mm. Interclavicle has a probable length of 520 mm., width anteriorly 360 mm., width of stem 120-240 mm.

Humerus, ulna, radius, manus, pelvis and femur unknown.

Length of tibia 248 mm., and of fibula 240 mm.

The intermedium is strong and the fibulare a thin bone.

Type: Transv. Mus. 212. Right scapulo-coracoid, right and part of left clavicle, part of the right cleithrum, part of interclavicle, right tibia, fibula, intermedium and fibulare, associated with a good skull. Abrahamskraal, Prince Albert. Low *Tapinocephalus* zone. Coll. van Hoepen.

Jonkeria angusticeps (Broom)

In our collection there is no specimen referable to this species. Broom's (14) figure of the ischium of the type is very misleading. With our increased knowledge it is now evident that of the ischium figured by Broom nearly half of the bone, viz. that part forming the contact with the pubis, is missing and what Broom figured was the dorso-posterior part only.

Type: A.M.N.H. 5633. A very imperfect ischium, associated with a good lower jaw. Abrahamskraal, Prince Albert. Low *Tapinocephalus* zone. Coll. van der Byl.

Jonkeria crassus (Broom)

With no specimen in our collection the following characterisation is extracted from Broom's (14) account.

The scapula is simply mentioned but not described by Broom.

The humerus is relatively short (440 mm.), very massive, with greatly expanded ends (proximal 345 mm. and distal 322 mm.); the shaft is very short and broad (135 mm.); the delto-pectoral crest is very long and powerful and nearly reaches the plane of the entepicondylar foramen; the caput is

widely oval; the processus medialis lies well distal of the plane of the caput; the capitellum is strong, thick and well modelled and extends very far proximally along the ventral surface right up to the plane of the entepicondylar foramen; the L.M.L. is strong with a strong swelling on the dorsal surface of the shaft; the entepicondyle is very strongly developed as a thick flange, with the ventral opening of the foramen large and broadly oval, and it lies well away from the edge of the bone, nearly under the base of the delto-pectoral crest; the ectepicondyle is developed as a thick sheet of bone, pierced obliquely by the small rounded foramen lying near the edge of the bone.

The ulna is massive; the width over the coronoid process is 217 mm.

The ilium is not figured or described by Broom.

Type: A.M.N.H. 5577. Scapula, humerus, part of ulna and ilium, associated with the dentaries. Kruidfontein, Prince Albert. Low *Tapinocephalus* zone. Coll. van der Byl.

Jonkeria haughtoni (Broom)

With about a dozen specimens in the collection a fairly full characterisation of this species can be given.

The scapula is high to very high (590-665 mm.), with the upper part of the blade broad to very broad (300-360 mm.); the tricipital ridge is fairly to quite prominent; the glenoidal facet of the scapula faces mainly postero-ventrally and but slightly outwards; the precoracoid forms the anterior part of the rim of the glenoid. The massive coracoid has a large glenoidal facet facing much externally.

The clavicle is represented by the upper half of the right clavicle; the upper end is moderately expanded (less than in *Parascapanodon*), with its antero-dorsal corner produced as a process, which overlies the lower end of the cleithrum, fitting into a groove in that bone, it has a strongly constricted waist and its lower end is probably well expanded.

The cleithrum is a long (440? mm.) fairly slender bone, with its dorsal end spatulate; in its lower half the posterior two-thirds of the outer face is grooved for the reception of the clavicle; the inner face is excavated along its posterior edge and in this recess the edge of the scapula fits. The cleithrum extends dorsally of the upper edge of the scapula.

The interclavicle is not preserved.

The humerus is massive but fairly short (456 mm.); the proximal expansion is very great (width 324 mm.) and the distal end is also wide (306 mm.); the shaft is very short and very broad (diams. 168 × 114 mm.);

the delto-pectoral crest is very long and nearly reaches the plane of the entepicondylar foramen; the caput is oval in outline; the processus medialis lies in a plane well distally of the plane in which the caput lies; the processus lateralis forms the most proximal point of the humerus; the capitellum is strong, thick, well modelled, and it extends proximally along the ventral face to reach the plane in which the entepicondylar foramen lies; the twist on the shaft is moderate (10°); the L.M.L. is well developed with a strong swelling on the dorsal surface of the shaft; the A.D.V.L. is strongly developed; the entepicondyle is strongly developed as a thick plate of bone, with the ventral opening of the foramen large and broadly oval, and it is situated far away from the edge of the bone; the ectepicondyle is developed as an outflaring thick sheet of bone pierced obliquely by a small foramen lying well away from the edge of the bone.

The ulna is large and massive (length 402 mm.), wide over the coronoid process (222 mm.); the dorsal rim to the sigmoid face is strong and prominent.

The radius is a large (length 320 mm.) robust bone with a strong proximo-postaxial flange for the biceps.

The manus is unknown.

In the pelvis the supra-acetabular part of the ilium is high (280 mm.) and relatively short (380? mm.), with the height thus 73% of the length; although not fully preserved the anterior iliac process appears to have been fairly short, but fairly high and fairly strongly everted; the posterior iliac process is short, with its postero-ventral edge folded over to form a fairly low and fairly weak oblique ilio-fibularis ridge, which is only slightly thickened in its upper part. The pubes are not preserved and both ischia are incomplete but these appear to have been short.

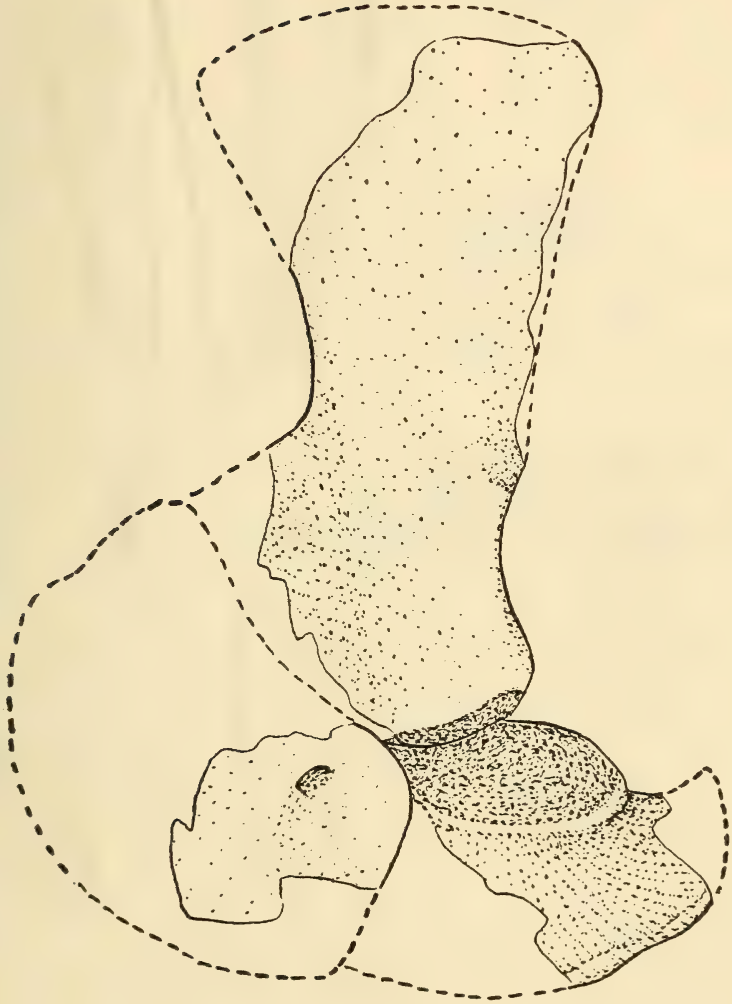
Both the femur and tibia are too inadequately preserved to merit a description.

The fibula is of moderate robustness and length (294 mm.); the distal end is rather weak and flattened.

The pes is not preserved.

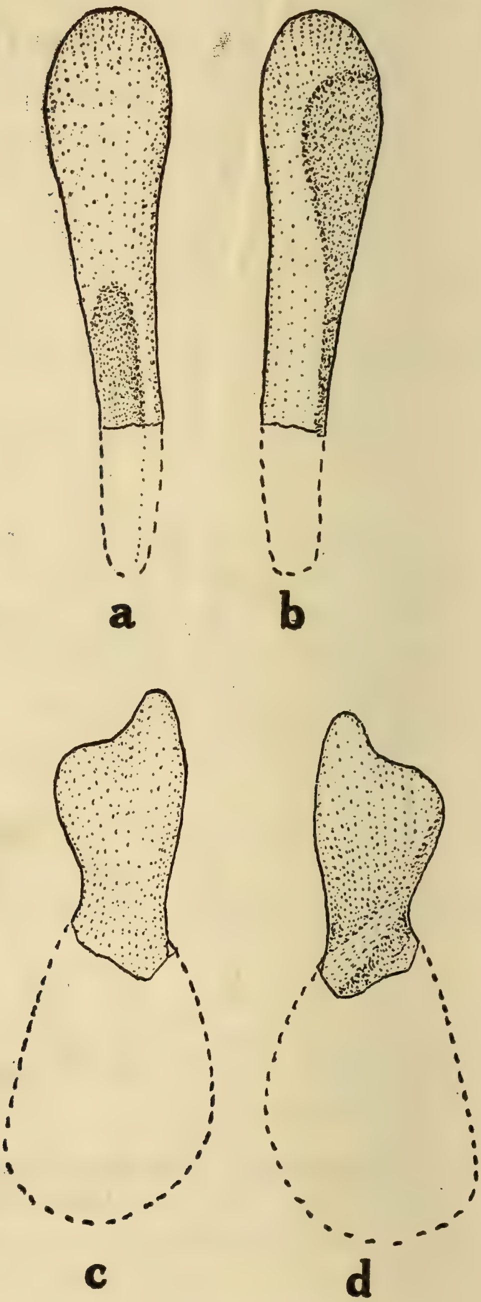
Type: S.A.M. 4343. An imperfect scapula, coracoid and precoracoid (Fig. 75); an imperfect right clavicle (Fig. 76 c-d) and right cleithrum (Fig. 76 a-b); a good right and an imperfect left humerus (Fig. 77); a good left ulna (Fig. 78 a, a^1); the distal end of a radius; an incomplete pelvis (Fig. 79); an imperfect femur; the proximal end of a tibia and a good fibula (Fig. 80), associated with a fairly good skull. Welgemoed, Prince Albert. Low *Tapinocephalus* zone. Coll. Haughton.

Fig. 75.



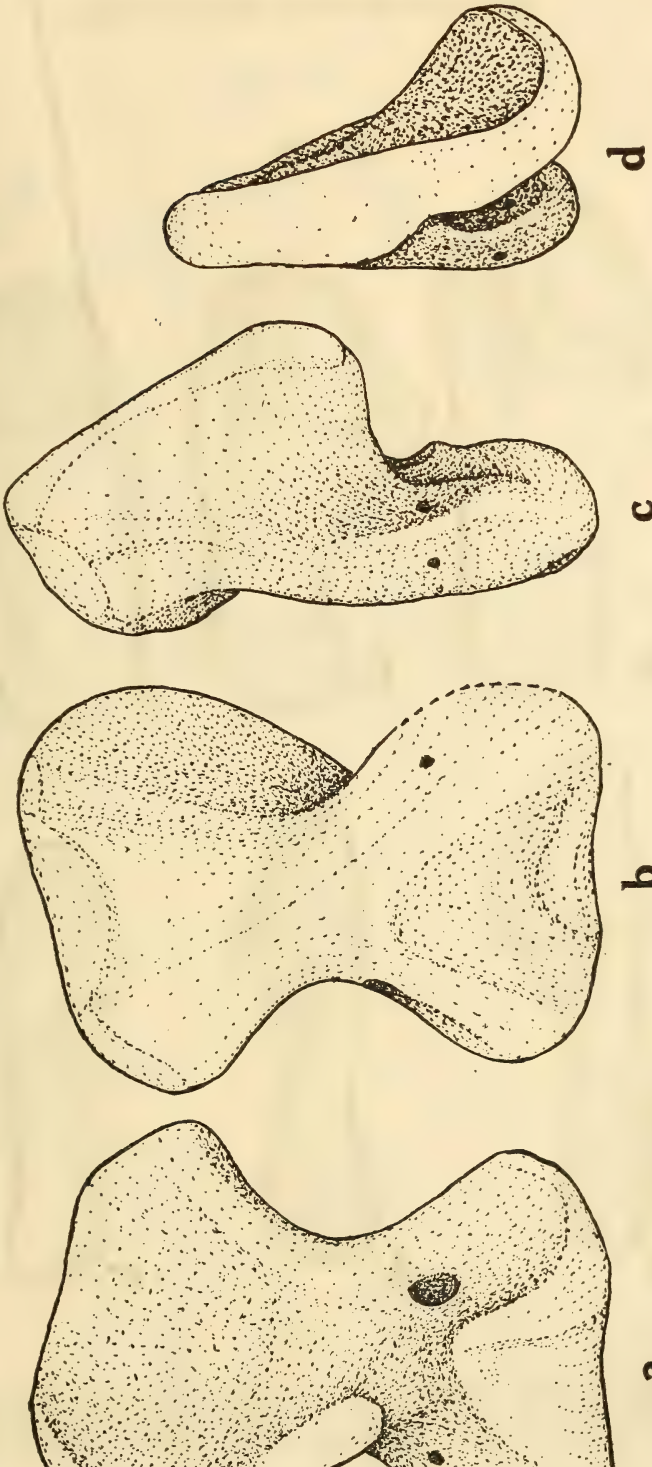
Scapulo-coracoid of *Jonkeria haughtoni*. S.A.M. 4343. (× $\frac{1}{6}$.)
Lateral view.

Fig. 76.



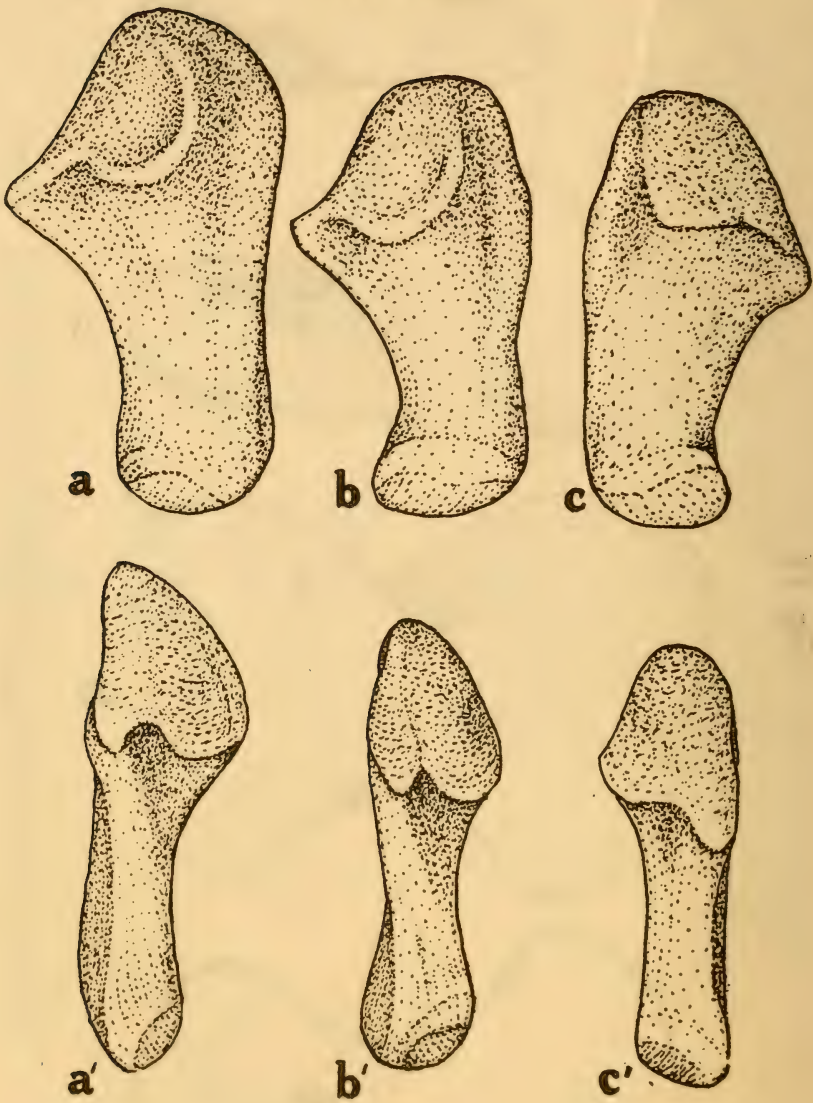
Jonkeria haughtoni. S.A.M. 4343. ($\times \frac{1}{8}$.) a. Outer view of right cleithrum. b. Inner view of right cleithrum. c. Outer view of right clavicula. d. Inner view of right clavicula.

Fig. 77.



Humerus of *Jonkeria haughtoni*. S.A.M. 4343. ($\times \frac{1}{6}$.) a. Ventral view. b. Dorsal view. c. Anterior view. d. Proximal view.

Fig. 78.



Ulnae of *Jonkeria haughtoni*. ($\times \frac{1}{6}$.) a and a¹. Dorsal and anterior views of S.A.M. 4343. b and b¹. Dorsal and anterior views of S.A.M. 11464. c and c¹. Dorsal and anterior views of S.A.M. 9002.

Fig. 79.

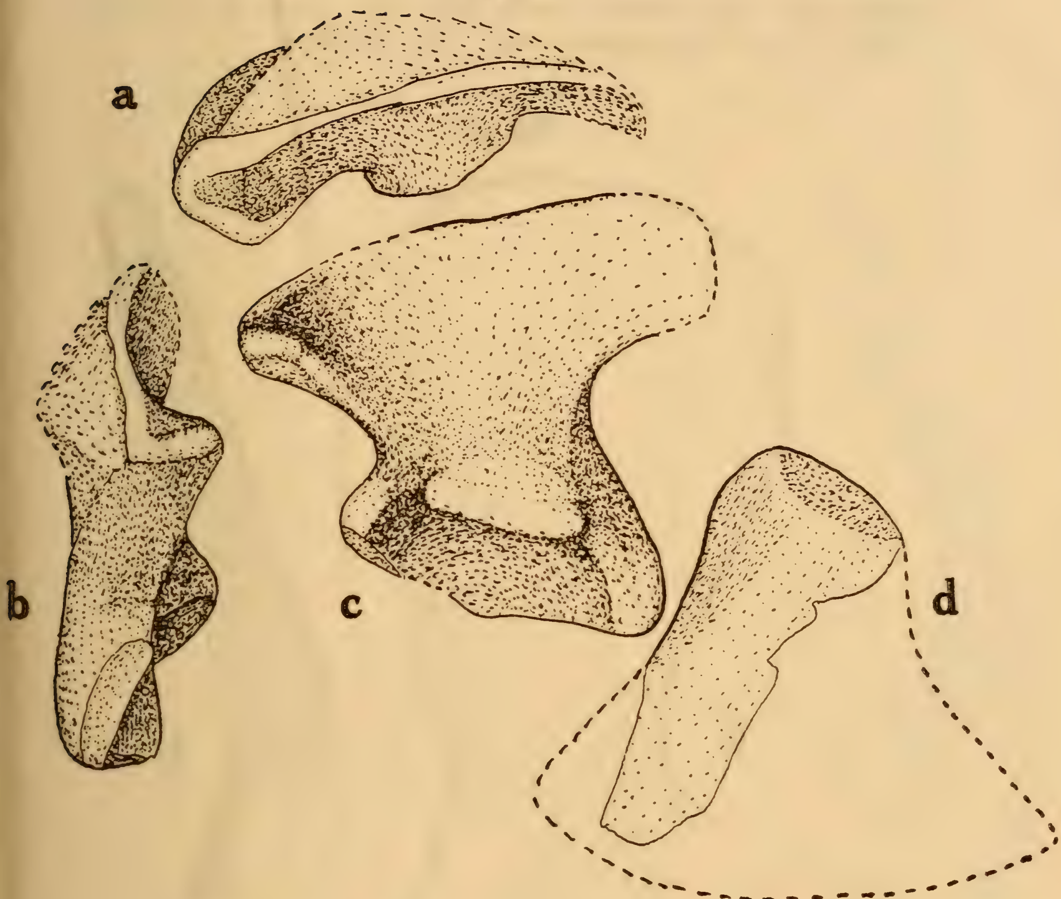
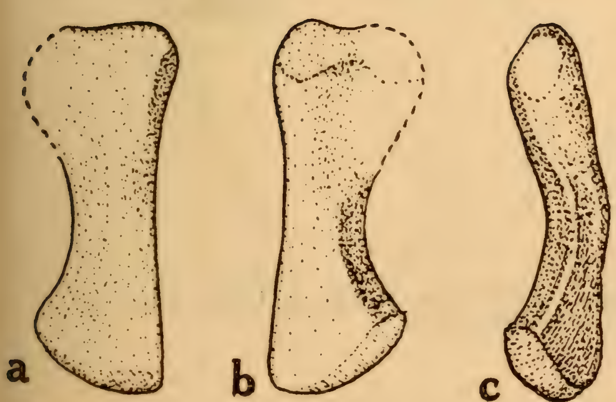


Fig. 80.



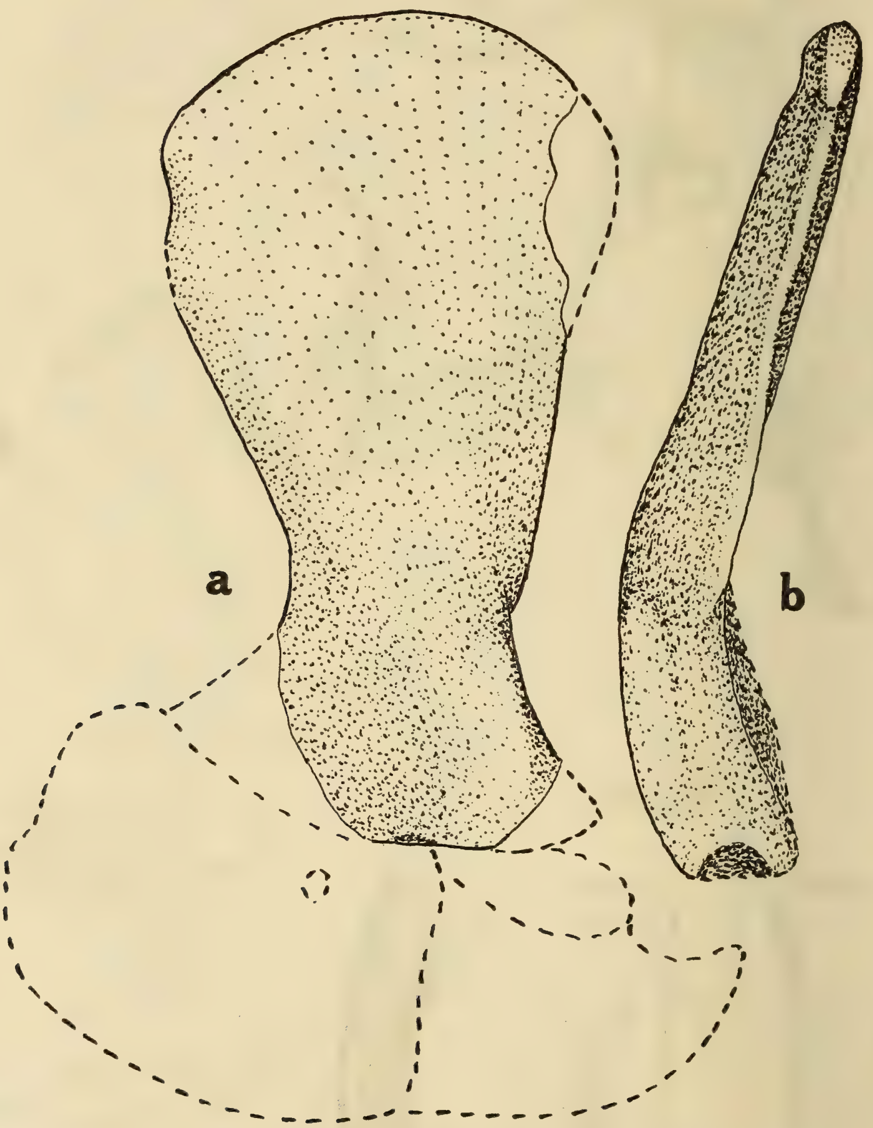
Above: *Jonkeria haughtoni*. S.A.M. 4343. ($\times \frac{1}{6}$.) a. Ilium in dorsal view. b. Ilium in posterior view. c. Ilium in lateral view. d. Ischium in lateral view.

Left: Right fibula of *Jonkeria haughtoni*. S.A.M. 4343. ($\times \frac{1}{8}$.) a. Dorsal view. b. Ventral view. c. Anterior view.

Referred specimens in the S.A.M. collection:

S.A.M. 4342. An isolated scapula (Fig. 81). Leeurivier, Beaufort West. Low *Tapinocephalus* zone. Coll. Haughton.

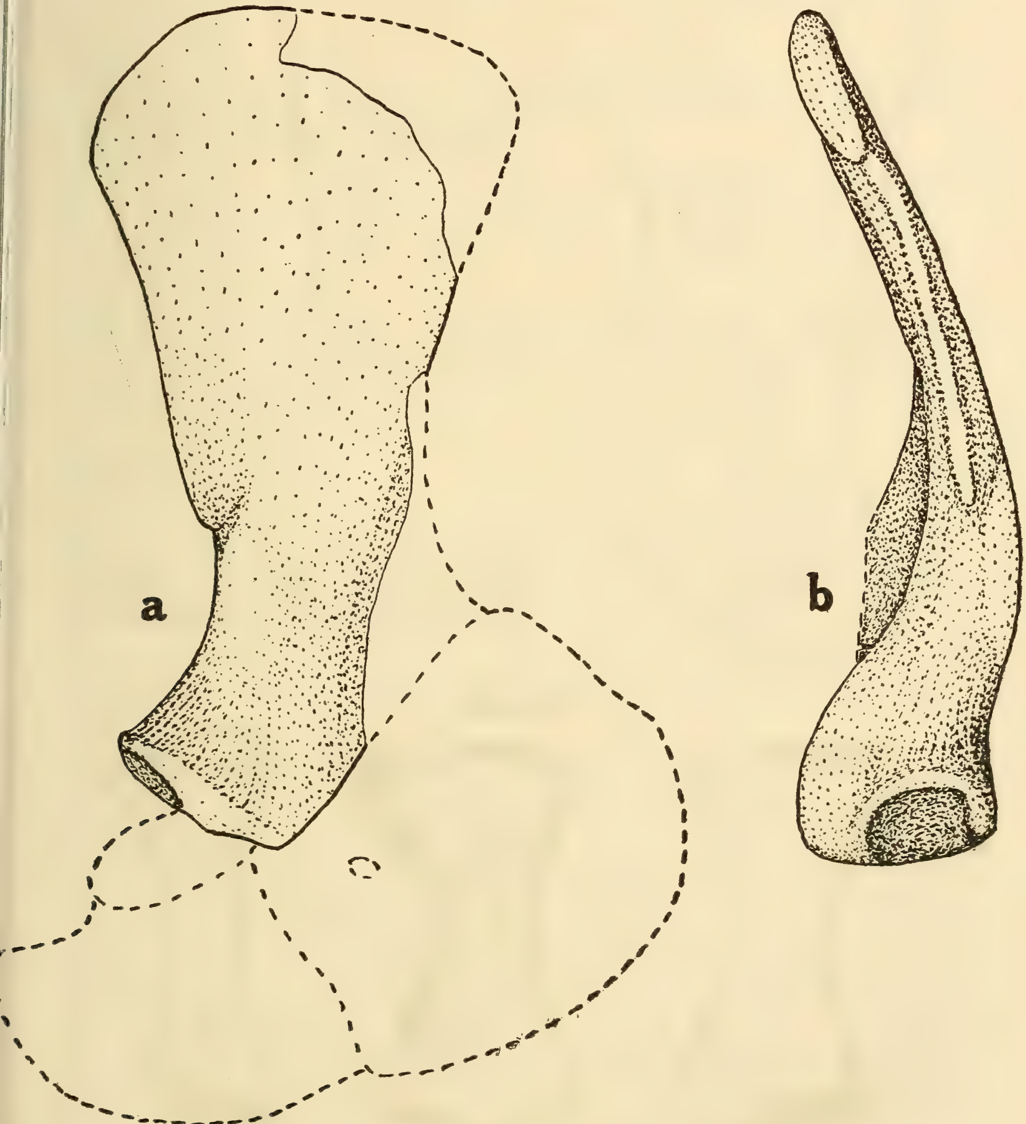
Fig. 81.



Scapula of *Jonkeria haughtoni*. S.A.M. 4342. (× ⅛.) a. Lateral view. b. Posterior view.

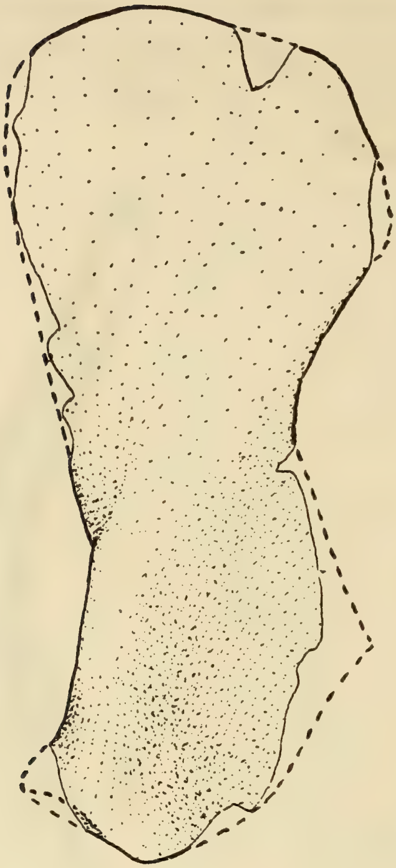
S.A.M. 9002. An isolated scapula (Fig. 82) and a distorted ulna (Fig. 78 c, c'). In outline the posterior border of the scapula has a distinctive step also shown in S.A.M. 4342, and probably also in the type where this edge is not preserved. Klein-Koedoeskop, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

Fig. 82.



Scapula of *Jonkeria haughtoni*. S.A.M. 9002. (× $\frac{1}{6}$.) a. Lateral view. b. Posterior view.

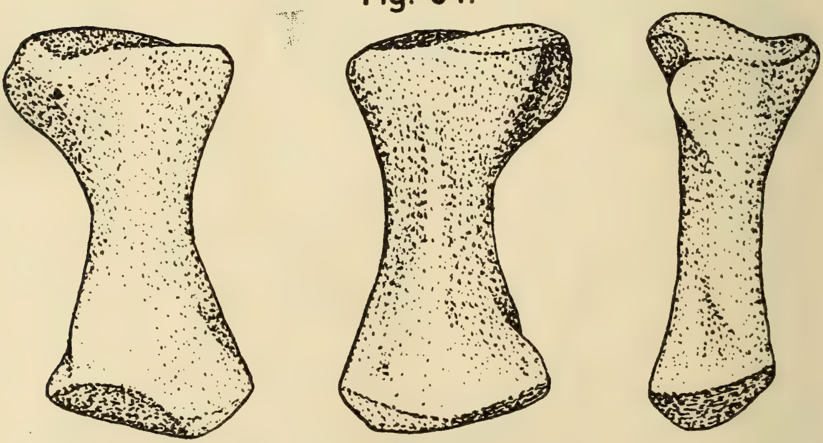
Fig. 83.



Left: Scapula of *Jonkeria haughtoni*. S.A.M. 11297. ($\times \frac{1}{6}$.) Lateral view.

Below: Right radius of *Jonkeria haughtoni*. S.A.M. 9145. ($\times \frac{1}{6}$.) a. Dorsal view. b. Ventral view. c. Posterior view.

Fig. 84.



a b c

S.A.M. 11297. An isolated scapula (Fig. 83). Boesmansrivier, Beaufort West. Mid *Tapinocephalus* zone. Coll. Boonstra.

S.A.M. 9009. An isolated precoracoid. This medium-sized bone, composed of a thin sheet except at the apex, where the sutural faces for the coracoid and scapula are fairly strong, is very similar to that of *J. truculenta* but larger, and is probably that of *J. haughtoni*. Klein-Koedoeskop, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

S.A.M. 9145. A good radius (Fig. 84) and an incomplete pubis probably belong to this species. Seekoeivlei, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

S.A.M. 9147. An isolated ulna with a damaged proximal end agrees sufficiently well with that of the type to be included in this species. Seekoeivlei, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

S.A.M. 11464. A very well preserved ulna (Fig. 78 b, b^1); although somewhat shorter than that of the type it can safely be included in this species. Koedoeskop, Beaufort West. Mid *Tapinocephalus* zone. Coll. Boonstra and Avenant.

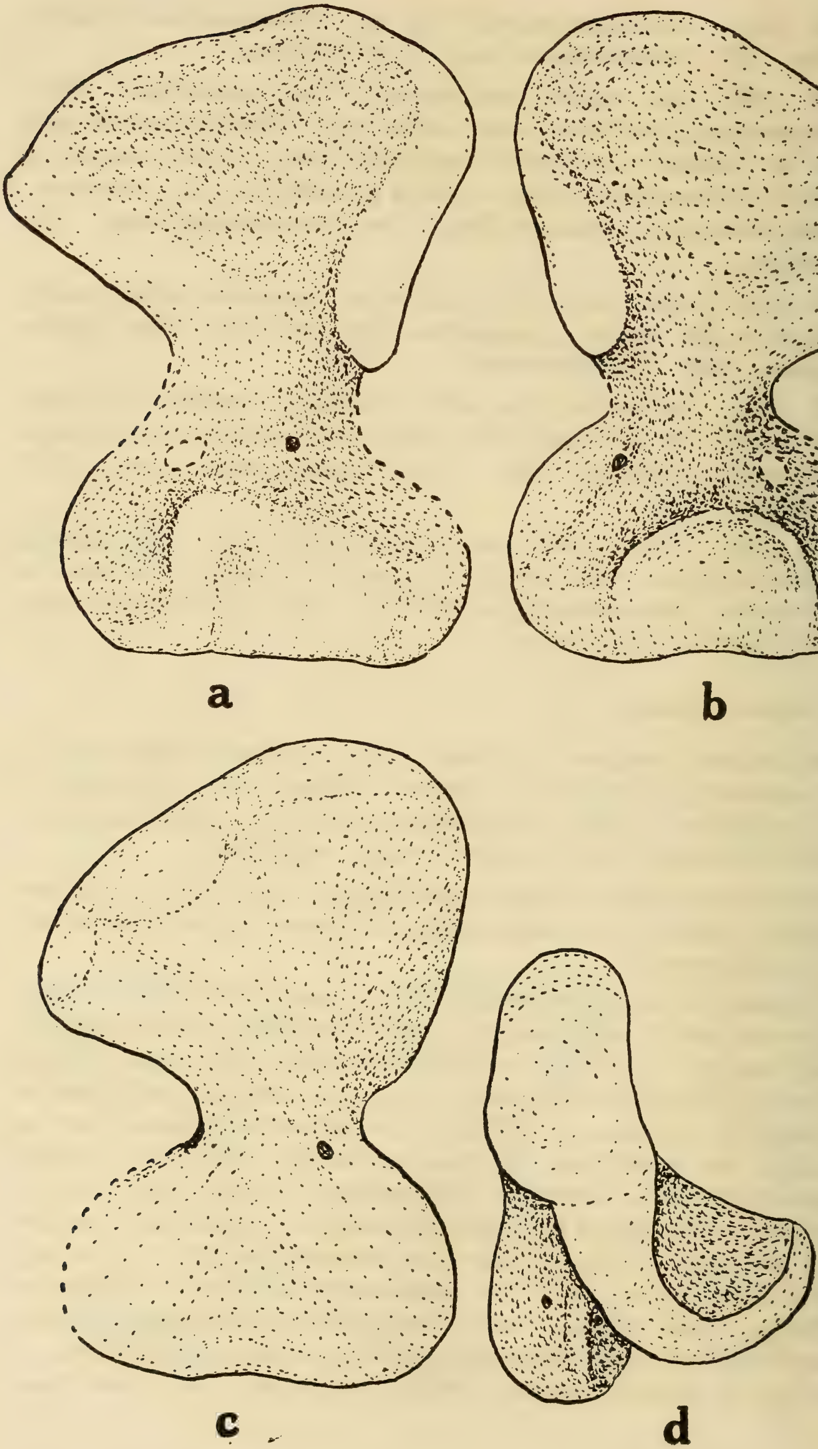
Jonkeria ingens (Broom)

In the specimen described by Broom (14) as *Jonkeria pugnax* but by me (1) considered a synonym of *Jonkeria ingens* Broom mentions the scapulae but without figuring or describing them; and of the humerus he states that it resembles that of *Jonkeria crassus* very closely.

In this collection there are four humeri, which in point of size can best be tentatively referred to this large species of *Jonkeria*, rather than to any other of the Titanosuchids.

The humerus in these specimens is large, massive, but not very long (length 504-510 mm.); both ends are greatly expanded (proximal 330-336 mm., and distal 312?-324 mm.); the shaft is short and broad (diams. 130-156 × 110 mm.); the delto-pectoral crest is long and powerful, but terminates well proximal of the plane in which the entepicondylar foramen lies; the caput is large and widely oval; the processus medialis lies very far distally of the plane in which the caput lies; the capitellum is strong, thick and very well modelled and it extends far proximally along the ventral face, but does not reach the plane of the entepicondylar foramen; the L.M.L. is strong; the A.D.V.L. is not very sharp; the entepicondyle is strongly developed as a thick flange of bone, with the ventral opening of the entepicondylar foramen fairly large and oval, lying fairly near the edge of the bone well removed from the base of the delto-pectoral crest; the ectepicondyle is a flaring sheet

Fig. 85.



Humeri of *Jonkeria ?ingens*. (× $\frac{1}{8}$.) a. S.A.M. 3433. Ventral view. b. S.A.M. 738. Ventral view. c. S.A.M. 738. Dorsal view. d. S.A.M. 738. Proximal view.

of bone pierced vertically by the small foramen lying well away from the edge of the bone.

Referred specimens:

A.M.N.H. 5608. Much of two scapulae and a humerus, associated with a skull. Kookfontein, Prince Albert. Mid *Tapinocephalus* zone. Coll. van Wyk.

S.A.M. 738. A good isolated humerus (Fig. 85 b-d). Gamka River. Low? *Tapinocephalus* zone. Coll. Cloete.

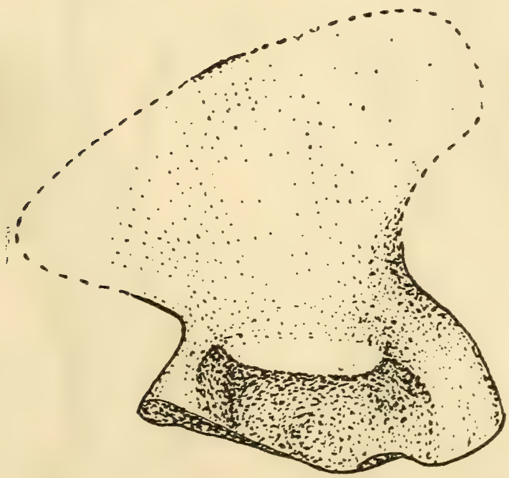
S.A.M. 3433. A good isolated humerus (Fig. 85a). Janwillemsfontein, Prince Albert. Low *Tapinocephalus* zone. Coll. Haughton.

S.A.M. 9006. An isolated proximal half of a humerus. Klein-Koedoeskop, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

S.A.M. 11994. An incomplete isolated humerus with a good distal end. Welgemoed, Prince Albert. Low *Tapinocephalus* zone. Coll. Haughton.

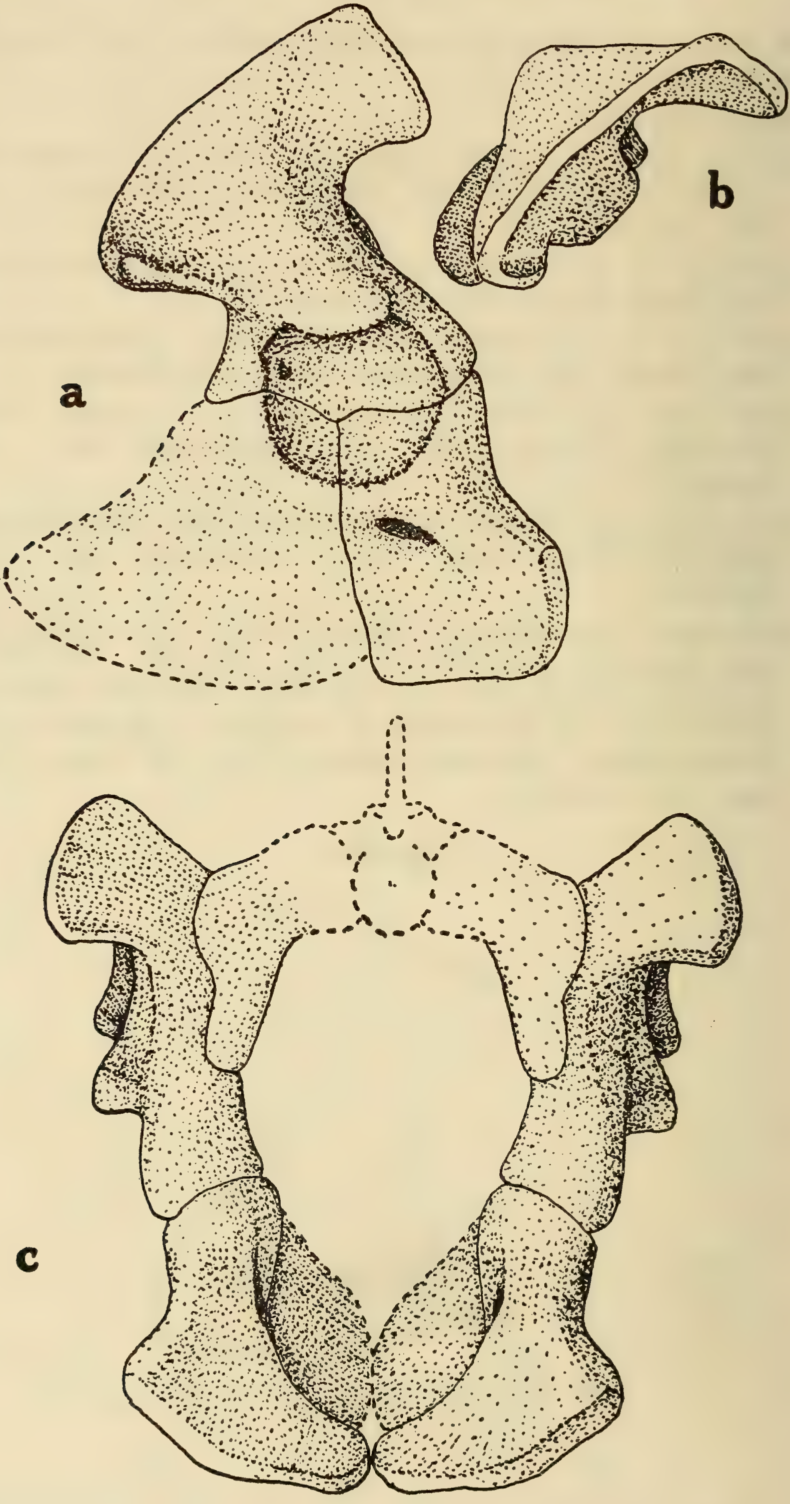
S.A.M. 9348. An incomplete and distorted humerus and an ilium lacking both the anterior and posterior processes (Fig. 86). The ilium is larger and more strongly built than those of the other species of *Jonkeria* and may provisionally be considered to represent that of *Jonkeria ingens*. Mierfontein, Beaufort West. Mid *Tapinocephalus* zone. Coll. Boonstra.

Fig. 86.



Ilium of *Jonkeria ?ingens*. S.A.M. 9348. (× ⅛.) Lateral view.

Fig. 87.



Jonkeria koupensis. S.A.M. 9004. ($\times \frac{1}{8}$.) a. Pelvis in lateral view. b. Ilium in dorsal view. c. Pelvis in anterior view.

Jonkeria koupensis Sp. Nov.

This new species appears to be very closely related to *J. haughtoni*, but the differences in the pelvis, as will be evident from the accompanying characterisation, warrant treatment as a distinct form.

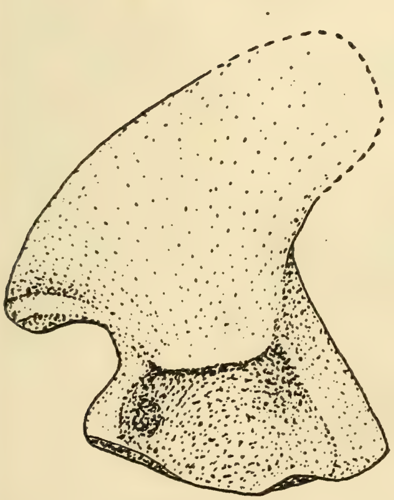
In the pelvis the pubo-ischiadic plate is probably short (83% of the height as reconstructed); the supra-acetabular part of the ilium is high (264 mm.) and the antero-posterior length of the iliac blade is very short (282 mm.), so that the height is 93% of the length; the anterior iliac process is fairly short, but appears shorter than it really is because of its strong eversion antero-laterally, and is fairly high; the posterior process is short and fairly low, with its postero-ventral edge moderately strongly folded over to form a fairly strong ilio-fibularis ridge on the outer face; this ridge is directed obliquely upwards, with its upper end not strongly bulbously thickened; a slight groove on the inner face of the everted anterior iliac process indicates the attachment of a rib anterior to the main sacral rib; antero-posteriorly the outer face of the iliac blade is deeply concave.

The antero-ventral edge of the pubis is strongly everted, with the tuberculum pubis confluent with the thickened part of the antero-ventral edge, which stretches to the median line where the pubes meet, but do not form a real symphysis.

The ischium is not preserved but probably is as reconstructed.

The ulna has the distal two-thirds preserved; it is a massive bone with the dorsal lip of the sigmoid face developed into a massive swelling in its preaxial part.

Fig. 88.



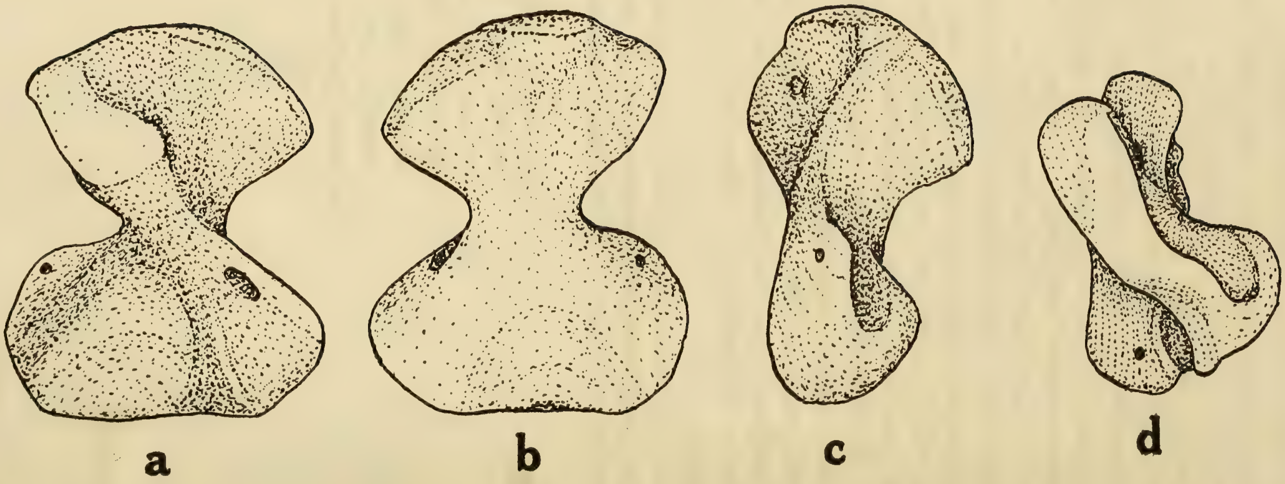
Illium of *Jonkeria koupensis*. S.A.M. 11983. (× ⅛.) Lateral view.

Type: S.A.M. 9004. A good pelvis, lacking only the ischia (Fig. 87) and the distal two-thirds of the ulna. Klein-Koedoeskop, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

Referred specimen:

S.A.M. 11983. An isolated ilium (Fig. 88). Abrahamskraal, Prince Albert. Low *Tapinocephalus* zone. Coll. Haughton.

Fig. 89.



Humerus of *Jonkeria parva*. S.A.M. 9149. ($\times \frac{1}{8}$.) a. Ventral view. b. Dorsal view. c. Anterior view. d. Proximal view.

Jonkeria parva Sp. Nov.

Although only a single isolated humerus is known, this bone is so distinctive that I do not hesitate to make it the type of a new species of *Jonkeria*.

This humerus is the smallest *Jonkeria* humerus as yet known; its length is only 312 mm., but it is a very massive element with both the proximal (222 mm.) and the distal (252 mm.) ends very greatly expanded; the shaft is very short and the bone is greatly constricted in the waist; the diameters of the shaft are 84 × 78 mm.; the delto-pectoral crest is fairly short and it terminates very far proximal of the plane in which the entepicondylar foramen lies; it has a very massive ventral edge and it terminates as a very thick knob. The caput is weak and its face is straplike, but it forms the most proximal part of the bone; the processus lateralis lies more distal than the caput; the processus medialis, as in all the Jonkerias, lies well distally of the caput; the capitellum is very massive indeed and it extends very far proximally along the ventral face, with its proximal border lying in a plane proximal to that in which the entepicondylar foramen lies; posteriorly of the well-modelled capitellum there is a deep groove in which the coronoid process moved when the ulna was flexed; the twist on the shaft is great (30°); the L.M.L. is distinct, with a large moundlike muscle scar on the dorsal surface of the shaft; the A.D.V.L. is very strong and forms a prominent ridge; the entepicondyle is strongly developed to form a greatly outflaring thick sheet of bone; the ventral opening of the entepicondylar foramen is oval and it lies well postaxially, near the edge of the bone; the ectepicondyle is developed as a greatly flaring thin sheet of bone penetrated in its thinner part, near the edge, by a small round ectepicondylar foramen.

Type: S.A.M. 9149. An isolated right humerus very well preserved (Fig. 89). Saairivier, Prince Albert. Low *Tapinocephalus* zone. Coll. Boonstra.

Jonkeria rossouwi Sp. Nov.

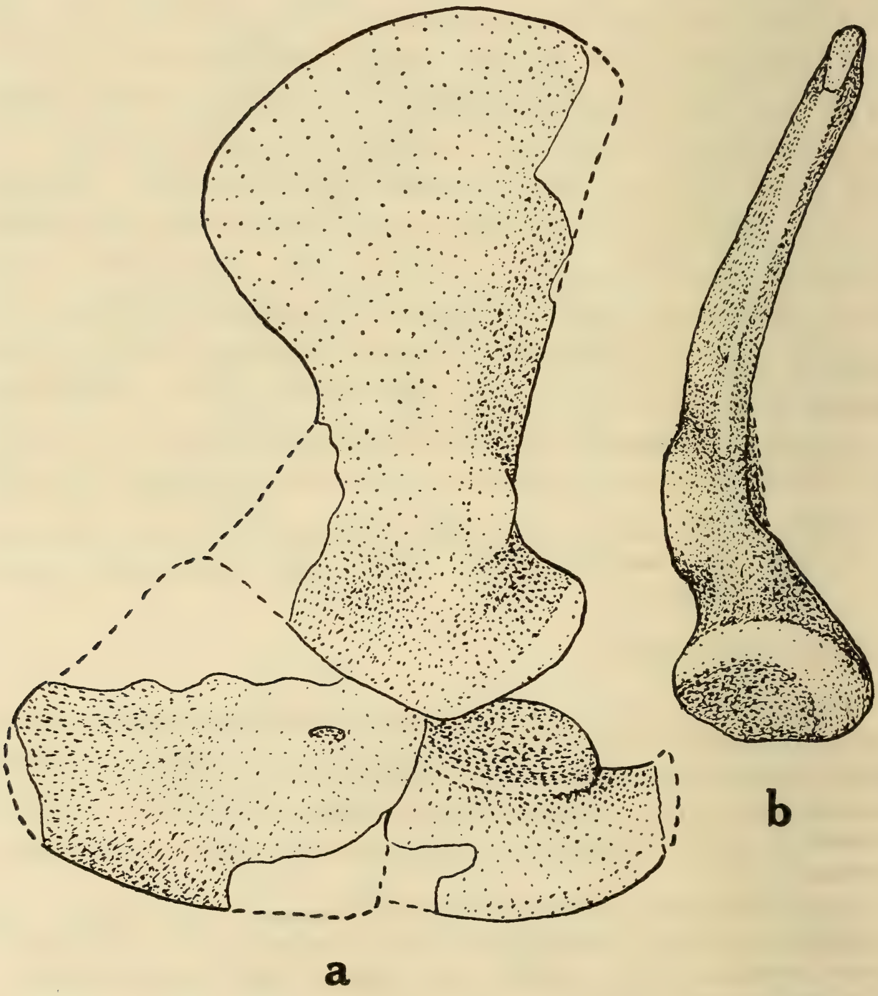
The specimen on which this new species is founded was found by Broom (14) to be different from the then known species of *Jonkeria,* but Broom, with a restraint unusual for him, did not name it. I am naming it *Jonkeria rossouwi* for Mr. P. J. Rossouw of the Geological Survey of the Union in recognition of the importance of his stratigraphical work on the *Tapinocephalus* zone.

In this species the pectoral girdle is fairly large and fairly massive. The scapula is fairly low (height 552 mm.) and the upper part of the blade is greatly expanded (width 324 mm.); the tricipital bulge is very prominent; the supra-glenoidal edge forms a strong raised rim; the internal opening of

the supracoracoid foramen opens into the deep subscapular groove; the glenoidal facet of the scapula faces ventro-posteriorly but not externally. The precoracoid is long but low (somewhat affected by crushing); the foramen pierces the bone very obliquely. The coracoid is small but massive, with a large glenoidal facet facing well externally.

The interclavicle is massive but short (480? mm.) with the stem wide posteriorly and with a narrowed waist anteriorly; the anterior spatulate end curves upwards very sharply and has a deep groove on its outer antero-

Fig. 90.



Jonkeria rossouwi. S.A.M. 5014. (× ⅛.) a. Scapulo-coracoid in lateral view
b. Scapula in posterior view.

lateral face for the reception of the postero-ventral edge of the clavicle; on the dorsal surface of the stem there is a strong medial ridge against which the precoracoids abut.

The clavicles and cleithrum are not known.

The humerus is fairly short (378 mm. in length), but massive with greatly expanded proximal (330 mm.) and distal (276? mm.) ends; the shaft is very short, thick and broad (132 × 84 mm.); the delto-pectoral crest is very long and nearly reaches the plane in which the entepicondylar foramen lies; the caput is broadly oval; the processus lateralis lies well proximally, in the same plane as the caput, whereas the processus medialis lies well distally; the capitellum is fairly massive and extends well along the ventral face and nearly reaches the plane of the entepicondylar foramen; the "twist" on the shaft is fairly small (15°); the L.M.L. is fairly strong with muscle scars on the dorsal surface of the shaft; the A.D.V.L. is well developed; the entepicondyle is strong with the ventral opening of the foramen large and nearly round; the ectepicondyle forms a thick flange pierced by the small foramen situated well away from the edge of the bone.

(The dorsal surface of the ectepicondyle shows a pathological lesion in the form of an irregular deep excavation and this is accompanied by a concomitant outgrowth of the olecranon of the ulna. In another humerus, that of *Phocosaurus* S.A.M. 11300, the disto-ventral face of the capitellum is deeply eroded with subsequent healing and the formation of a new but concave instead of a convex articulatory facet. (Osteitis fibrosa? Osteomalachia?))

The ulna has suffered pathological deformation so that the olecranon is proximally prolonged as a thick outgrowth. The normal ulna would appear to have had a more slender shaft and a weaker coronoid process than the other known species of *Jonkeria*.

The radius is only slightly pathologically deformed. Its length is 312 mm. and the flange on the proximo-postaxial corner is weak.

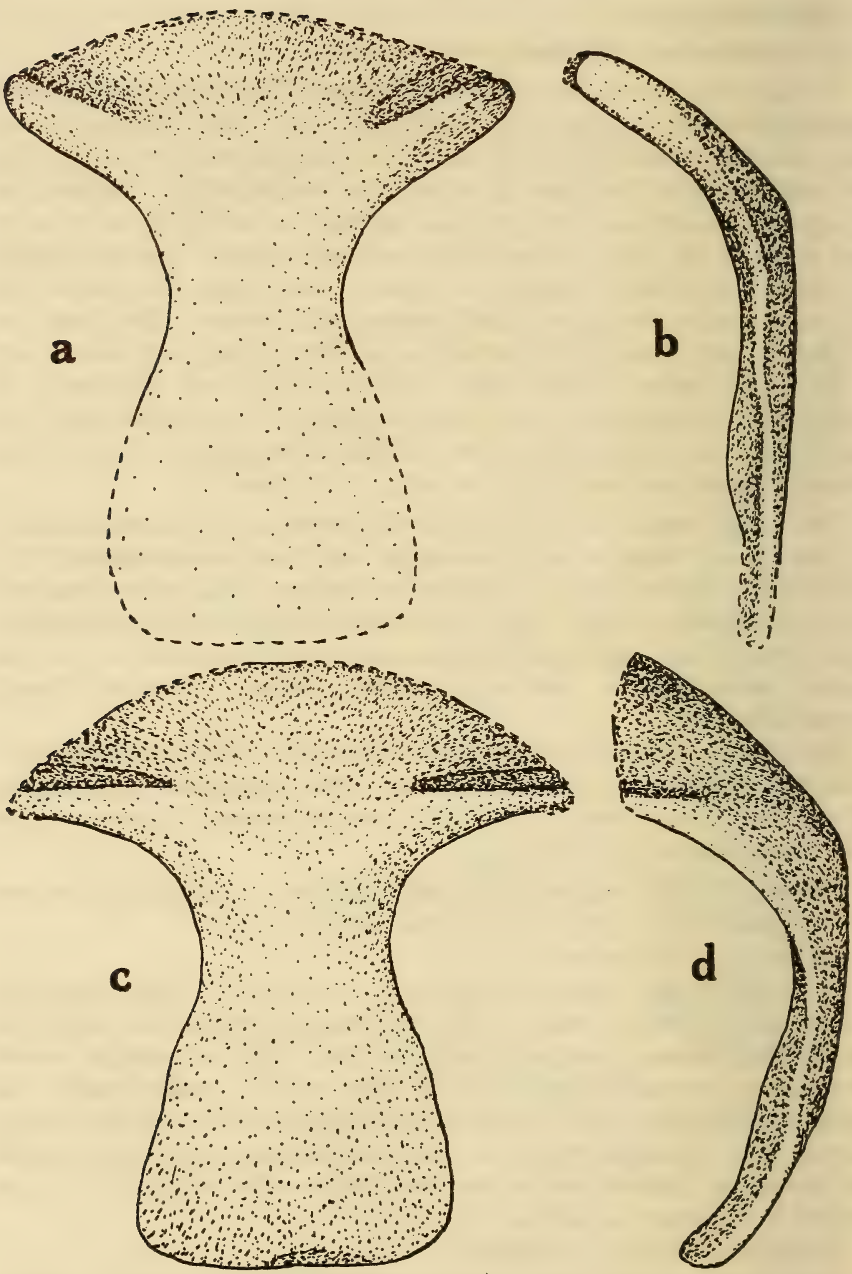
The manus is not known.

In the pelvis the supra-acetabular part of the ilium is high (288 mm.) and relatively short (336 mm.) so that the height is 87% of the length; the anterior iliac process is relatively short, but fairly high and strongly everted; the posterior process is short and fairly low, with its postero-ventral edge folded over strongly to form a strong vertical ridge, which is dorsally strongly bulbous, and it projects strongly laterally; on the inner face of the anterior iliac process no distinct facet is preserved for the attachment of a rib lying anterior to the main sacral rib.

No pubis or ischium is preserved.

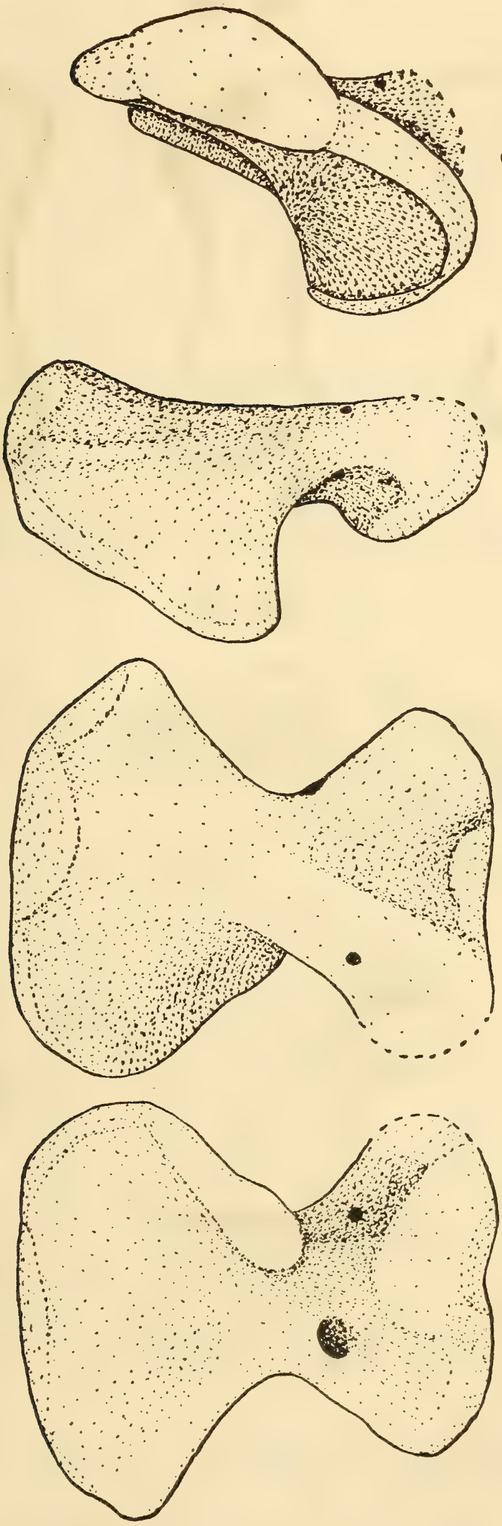
The femur is fairly long (504 mm.); fairly broad over the external trochanter (264 mm.), which is not separated by a notch from the proximal

Fig. 91.



Interclaviculae. (× ⅛.) a. *Jonkeria rossouwi*. S.A.M. 5014. Ventral view. b. *Jonkeria rossouwi*. S.A.M. 5014. Lateral view. c. *Jonkeria* sp. indet. S.A.M. 9124. Ventral view. d. *Jonkeria* sp. indet. S.A.M. 9124. Lateral view.

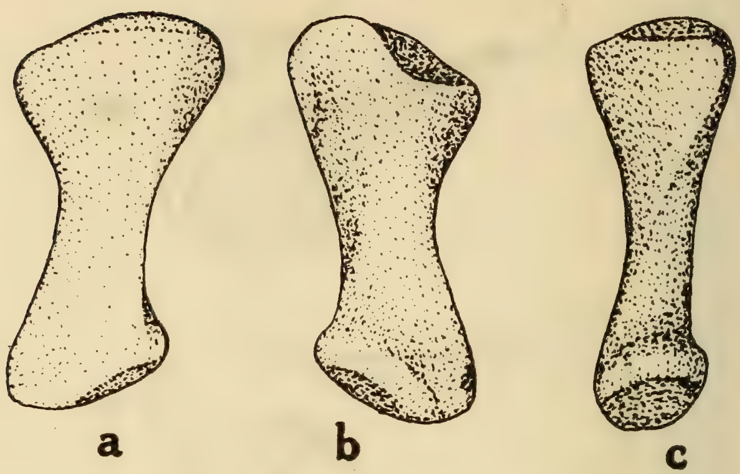
Fig. 92.



a b c d

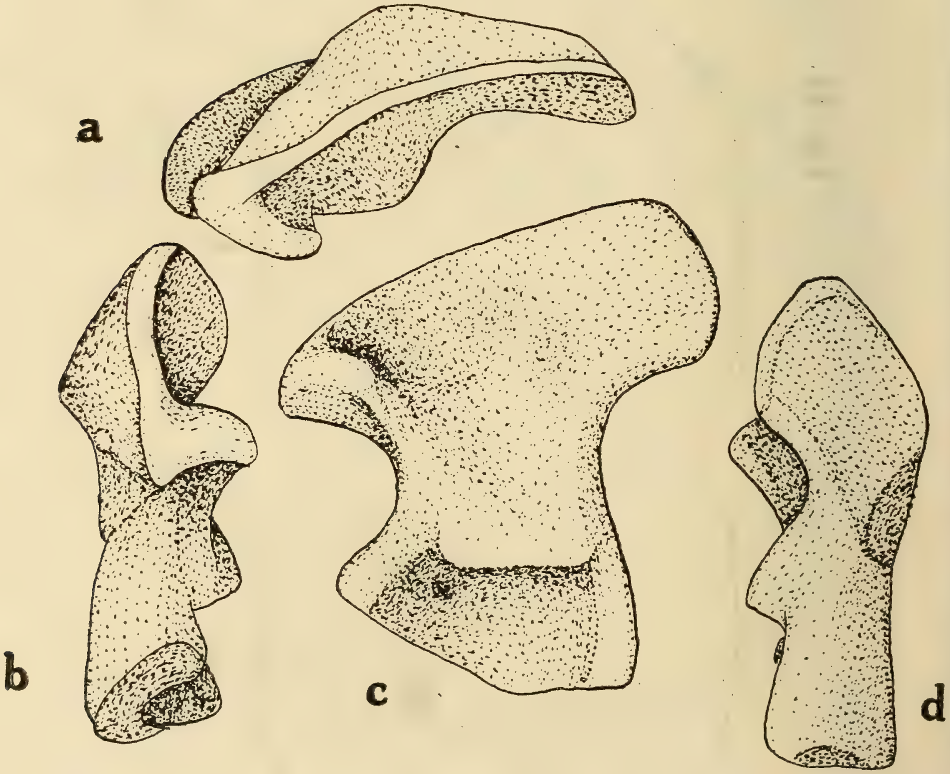
Humerus of *Jonkeria rossouwi*. S.A.M. 5014. (× 1/6.) a. Ventral view. b. Dorsal view. c. Anterior view. d. Proximal view.

Fig. 93.



Left radius of *Jonkeria rossouwi*. S.A.M. 5014. (× $\frac{1}{6}$.)
a. Dorsal view. b. Ventral view. c. Posterior view.

Fig. 94.



Right ilium of *Jonkeria rossouwi*. S.A.M. 5014. (× $\frac{1}{6}$.) a. Dorsal view.
b. Posterior view. c. Lateral view. d. Anterior view.

face; the caput is fairly thick (114 mm.) and is directed much preaxially; the shaft is broad but flat (diams. 156 × 84 mm.); the femoro-tibialis ridge is fairly strong; the distal facets of the femur are small and directed much distally, especially the ectepicondyle which lies far distally. (These features of the distal end of the femur, differing as they do from the other Jonkerias, appear to be due to some measure of pathological deformation.)

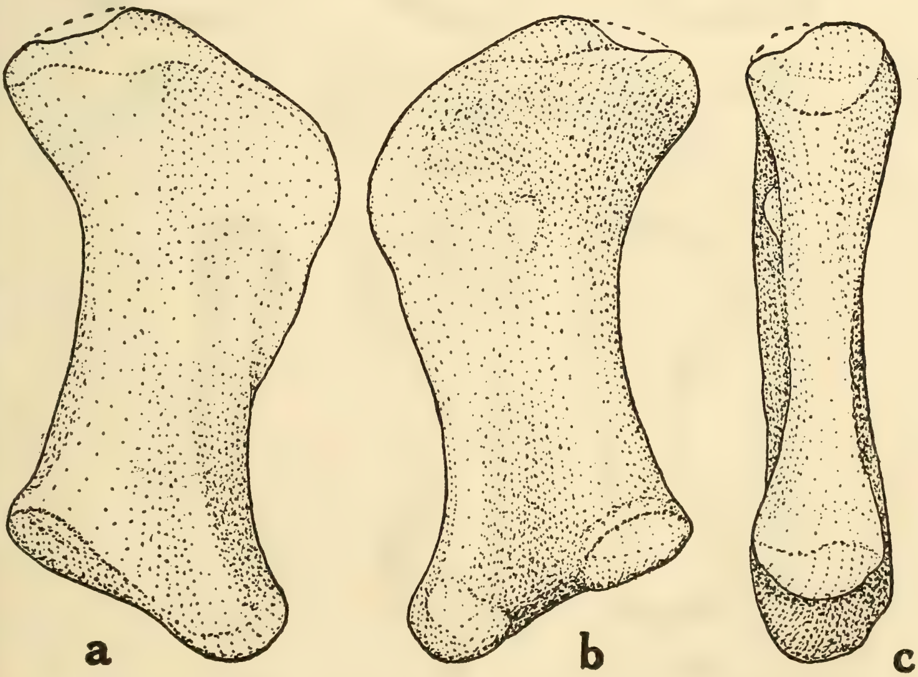
The tibia is fairly robust (length 300 mm.); the proximal face is inclined much postaxially to correspond with the distally situated postaxial facet of the femur.

The fibula is fairly slender and long (330 mm.).

The pes is not known.

Type: S.A.M. 5014. The left scapula and incomplete precoracoid and coracoid (Fig. 90), an imperfect interclavicle (Fig. 91 a, b), a diseased left humerus (Fig. 92), a deformed left ulna and a left radius (Fig. 93), a right ilium (Fig. 94), a left femur (Fig. 95), a left tibia (Fig. 96) and a left fibula (Fig. 97). Abrahamskraal, Prince Albert. Low *Tapinocephalus* zone. Coll. van der Byl.

Fig. 95.



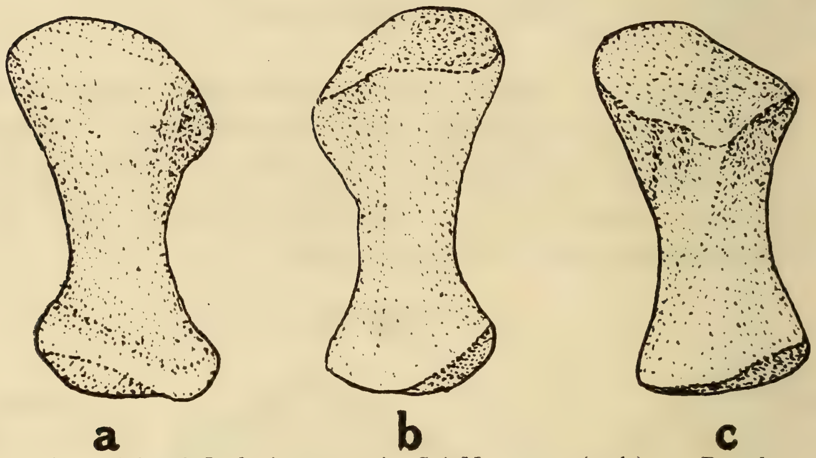
Left femur of *Jonkeria rossouwi*. S.A.M. 5014. (× 1/6.) a. Dorsal view. b. Ventral view. c. Anterior view.

Referred specimens:

S.A.M. 11979. An incomplete interclavicle (Fig. 98 a, b) and the proximal ends of an ulna and fibula. Kruisvlei, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

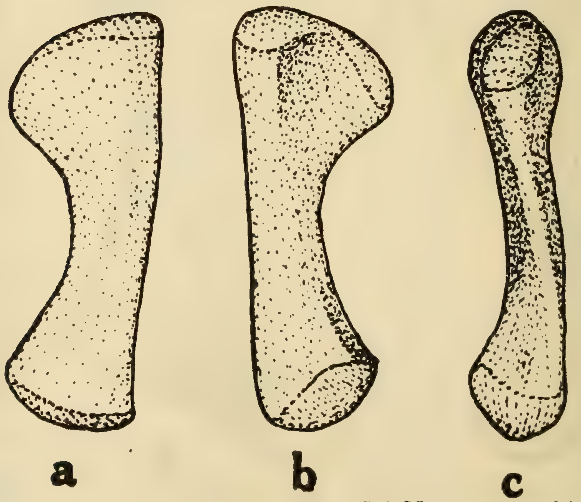
S.A.M. 11982. A fairly good interclavicle (Fig. 98 c, d). Abrahamskraal, Prince Albert. Low *Tapinocephalus* zone. Coll. Haughton.

Fig. 96.



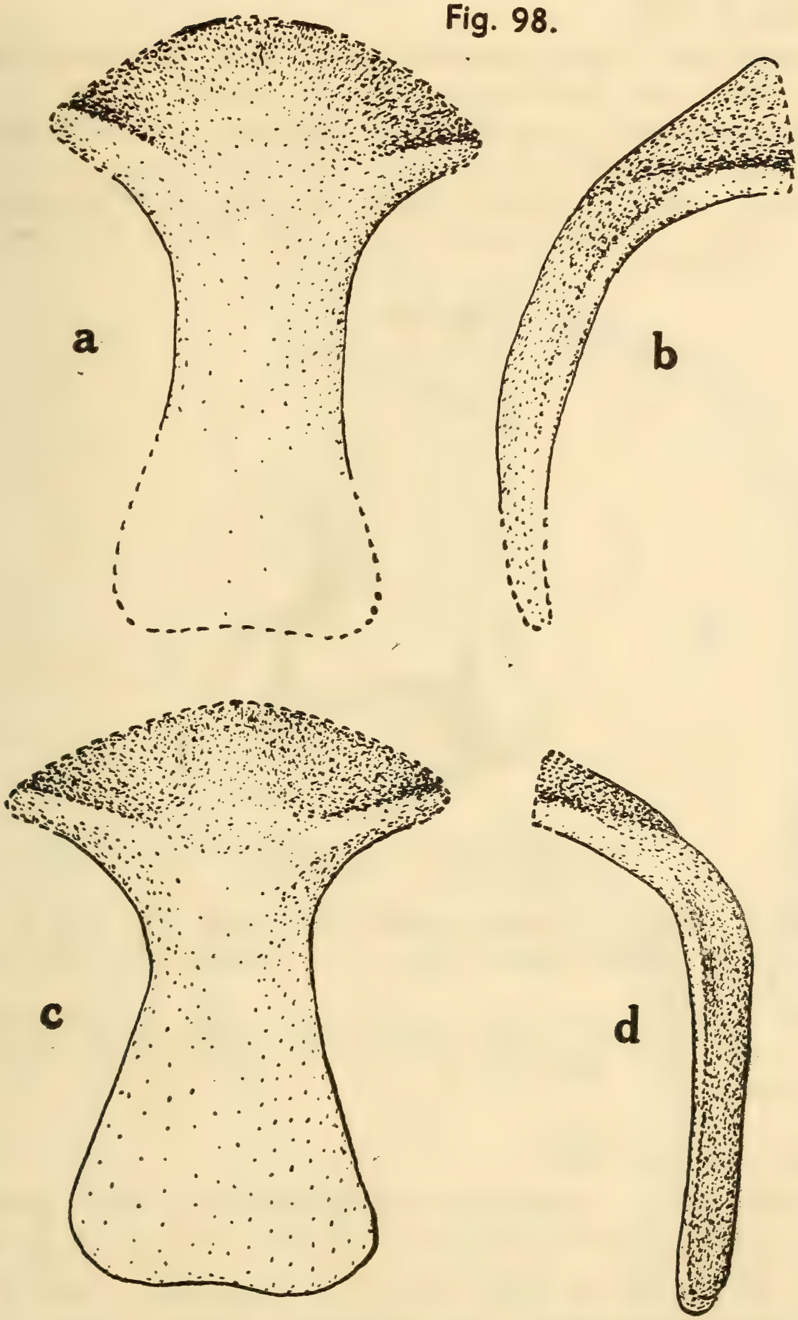
Left tibia of *Jonkeria rossouwi*. S.A.M. 5014. (× $\frac{1}{6}$.) a. Dorsal view. b. Ventral view. c. Posterior view.

Fig. 97.



Left fibula of *Jonkeria rossouwi*. S.A.M. 5014. (× $\frac{1}{6}$.) a. Dorsal view. b. Ventral view. c. Anterior view.

Fig. 98.



Interclaviculae of *Jonkeria rossouwi*. ($\times \frac{1}{6}$.) a. S.A.M. 11979. Ventral view. b. S.A.M. 11979. Lateral view. c. S.A.M. 11982. Ventral view. d. S.A.M. 11982 Lateral view.

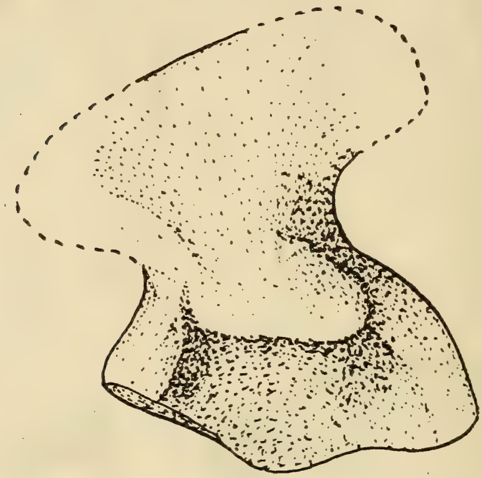
Jonkeria Sp. Indet.

S.A.M. 9124. A good interclavicle (Fig. 91, c, d). Voëlfontein, Prince Albert. Low *Tapinocephalus* zone. Coll. Boonstra.

This interclavicle is larger and stronger than those of the known species of *Jonkeria* and may thus possibly be *J. ingens*.

S.A.M. 11984. An imperfect isolated ilium (Fig. 99) of an unknown locality. It would appear to lie fairly close to the ilium of *J. haughtoni*.

Fig. 99.



Right ilium of *Jonkeria* sp. indet. S.A.M. 11984. (× ⅙.) Lateral view.

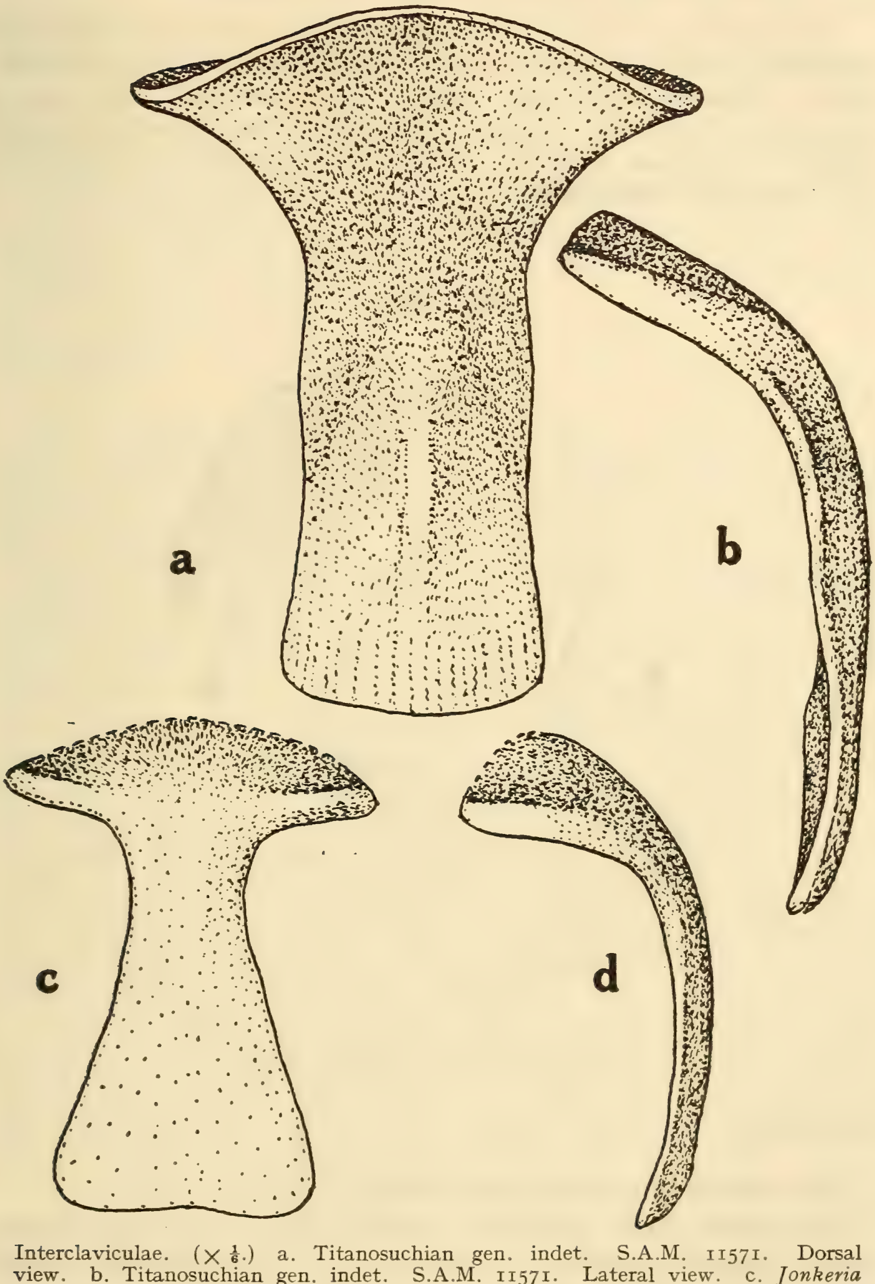
S.A.M. 11886. A nearly complete interclavicle (Fig. 100 c, d). Vindraersfontein, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

This small bone with a narrow waist and the strongly expanded posterior end of the stem is apparently of a small species of *Jonkeria* — possibly of *J. parva*.

Titanosuchia Genera Indet.

S.A.M. 11571. A large isolated interclavicle with a strongly upturned anterior end and a strong median keel on the dorsal face of the stem (Fig. 100 a, b). It has the long stem of the Tapinocephalians but the width is that usually seen in the Titanosuchians. Probably a large Titanosuchid. Klein-Koedoeskop, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

Fig. 100.

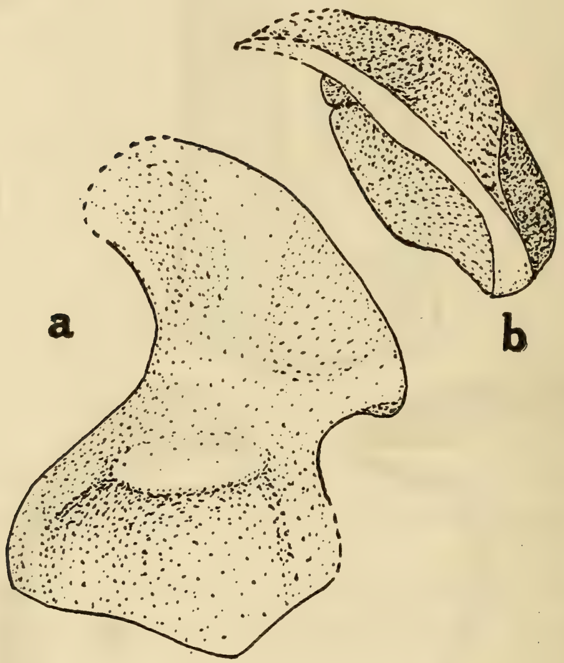


Interclaviculae. ($\times \frac{1}{6}$.) a. Titanosuchian gen. indet. S.A.M. 11571. Dorsal view. b. Titanosuchian gen. indet. S.A.M. 11571. Lateral view. c. *Jonkeria cf. parva.* S.A.M. 11886 Ventral view. d. *Jonkeria* cf. *parva.* S.A.M. 11886. Lateral view.

S.A.M. 11986. An isolated ilium (Fig. 101). Letjiesbos, Beaufort West. Mid *Tapinocephalus* zone. Coll. Boonstra.

This ilium has on the outer face of the posterior iliac process neither the horizontally placed ilio-fibularis ridge, usually seen in the Tapinocephalia, nor the obliquely placed ridge, usual in the Titanosuchia. The area of origin of the ilio-fibularis is rather a thickening of the postero-ventral edge without any eversion or folding over. In outline this ilium agrees more with those of the Titanosuchia.

Fig. 101.



Ilium of a ? Titanosuchian. S.A.M. 11986. (× ⅙.)
a. Lateral view. b. Dorsal view.

Anteosauria

Infra-ordinal Characters of the Girdles and Limbs.

The pectoral girdle is light; the scapular head of the triceps originates from a prominent tubercle; the outer face of the precoracoid is strongly convex and the glenoidal facet on the coracoid is bipartite.

The humerus is fairly light; without an ectepicondylar foramen; the radial condyle is well modelled, but situated well distally; both the processus lateralis and medialis lie far proximally; the delto-pectoral crest is very short and is directed much postaxially.

In the manus the carpal formula is 3, 1, 5, and the phalangeal formula 3, 3, 4, 4?, 2.

The iliac blade is low and the acetabulum faces much ventrally; the ilio-fibularis ridge lies horizontally; no supra-acetabular buttress is developed.

The femur is light, long and slender with the internal trochanter developed as a ridge; the width over the external trochanter is very small.

In the pes the tarsal formula is 2, 1, 5 and the phalangeal formula 2?, 3?, 3?, 4?, 2.

Anteosauridae

Family Characters of the Girdles and Limbs.

The Anteosaurid pectoral girdle is only imperfectly preserved in two specimens; but, even so, it is evident that the Anteosaurid girdle differs greatly from that of all the other Deinocephalia.

The girdle is of moderate size and is lightly built. No complete scapula is known but it would appear that it was of moderate width and height (455-475 mm. as reconstructed); instead of a tricipital mound or ridge, as in all the other Deinocephalia, there is developed (for the origin of the scapular head of the triceps) a prominent tubercle on the posterior edge of the scapula 25-35 mm. above the glenoidal edge; the internal opening of the foramen supracoracoideus opens into the fairly deep subscapular groove; the glenoidal facet of the scapula is large and faces ventro-posteriorly, but also much externally, and the outer and posterior margins are sharp, prominent and well moulded.

The coracoidal plate is fairly long antero-posteriorly. The precoracoid is relatively large; its dorso-posterior apex, just posterior to the outer opening of the foramen supracoracoideus, forms a fairly long margin to the glenoid; here the outer face of the precoracoid forms a decided depression or recess to house the processus lateralis of the humerus, when this bone is in its forward position; the foramen supracoracoideus penetrates the bone obliquely so that it internally forms a groove in the sutural face and thus opens into the subscapular groove; the outer precoracoidal face is strongly convex, so that its lower edge is directed much medially.

The coracoid is small and light, but greatly thickened where it houses the lower half of the glenoid; this facet is bipartite — the inner and posterior moiety receives the head of the humerus in its posteriorly disposed position, and the outer and anterior moiety receives the humerus when it is disposed

anteriorly; the inner part of the facet is directed dorso-posteriorly and slightly externally, whereas the outer part is directed much externally.

Nothing is known of the cleithrum, clavicula and interclavicula.

The humerus, known only in three specimens, is fairly lightly built and fairly small to medium (length 300?-375 mm.); the proximal expansion is fairly small (width 162-168 mm.); the distal expansion is somewhat greater (width 200-205 mm.); the shaft is fairly long and slender (diams. 76-84 × 48-65 mm.); the delto-pectoral crest is very short and terminates a considerable distance proximal to the ventral opening of the entepicondylar foramen, and is directed much postaxially; the caput is narrowly oval; the processus medialis lies in the same plane as the caput, whereas the processus lateralis lies a little further proximally; the radial condyle is situated distally, but extends a little along the ventral face and also curves on to the dorsal face; the "twist" on the shaft is large (40°); the L.M.L. is fairly definite and the A.D.V.L. is sharp and prominent; the entepicondyle is fairly greatly expanded, with the foramen entering dorso-postaxially and leaving as a ventral slit; the ectepicondyle is well expanded as a thin plate of bone housing on its ventral face a groove for the passage of the radial vessels.

The only radius known is a light, slender featureless bone and the only known ulna (length 260 mm.) is crushed flat.

The manus in the only specimen known has the carpal formula 3, 1, 5 and the phalangeal formula 3, 3, 4, 4?, 2.

The pelvis is only known from one imperfect ilium. This, however, shows that the Anteosaurids had an ilium of a type radically different from any known in the South African Deinocephalia. It is without the strong supra-acetabular buttress so typical of the Deinocephalia; instead, the acetabulum is dorsally bounded by a continuous curved ridgelike margin without a supra-acetabular notch; the thickly rounded posterior edge of the fairly short posterior process, from which the ilio-fibularis originates, lies horizontally as in the Tapinocephalia; the iliac blade was presumably short and low.

In Fig. 104 an orthoprojection, taken by pantograph, vertically on to the iliac part of the acetabulum (as is the case in all the figures showing the lateral aspect of the pelvis, i.e. a projection on to the median plane) is shown. But I believe that in the naturally articulated skeleton the iliac portion of the acetabulum, in this case, would be directed much more ventrally so that the disposition of the femur in the Anteosaurids would be radically different from the condition in all other Deinocephalia.

The femur of the Anteosaurids looks very different from that of the other Deinocephalians; although not very long (210-420 mm.) it appears very long because of its general slenderness and long shaft; the width over

the external trochanter is small and varies from 47 to 120 mm.; the shaft is narrow and has diameters ranging from 28 × 18 to 75 × 45 mm.; the external trochanter is situated far proximally and nearly in the same plane as the caput; the caput is short pre-postaxially and flows directly into the external trochanter; with the preaxial border deeply concave and the postaxial border convex the femur is a curved bone with the caput well preaxially and somewhat dorsally directed; the internal trochanter forms a low ridgelike tubercle situated well away from the preaxial face, with a resulting reduced inter-trochanteric fossa; the femoral condyles face much distally with the external one further distally than the internal one; the popliteal fossa is elongated; the epicondyles, in one specimen, form a thin sheetlike expansion, both pre- and postaxially; the femoro-tibialis ridge is weak and the area for the insertion of the ilio-femoralis is narrow; there is a strong ridge for the insertion of the pubo-ischio-femoralis internus.

The tibia is unknown.

The fibula is a lightly built long and slender bone with its proximal end strongly expanded and with the facets for the femur nearly terminal. Whereas the proximal end is flattened, the distal facet is broadly oval in outline; the preaxial face is fairly straight, whereas in the other Deinocephalia this is deeply concave.

The pes has the tarsal formula 2, 1, 5 and the phalangeal formula uncertain but probably 2?, 3?, 3?, 4?, 2.

Anteosauridae

The Family Characters are as for the infra-order.

Genus *Anteosaurus* Watson

In this genus the girdles and limbs are very inadequately known. The generic characters that can be determined from an incomplete scapula, an incomplete and distorted humerus, three coracoids, an incomplete ilium, two good and two incomplete femora are as follows: Tricipital tubercle elongated, 35 mm. above the edge of the glenoid; humerus fairly small (length 300? mm.); the shaft is slender (diams. 60 × 48 mm.); the ilium is as described for the infra-order; the femur is slender (length 402?-420 mm.); width across the external trochanter 108-120 mm.; the epicondyles with moderate or pronounced sheetlike expansions.

Anteosaurus acutirostris (Boonstra).

Femur 420 mm. in length, with flaring epicondyles.

S.A.M. 11977A. Two good femora (Fig. 102 a-c), associated with a good skull (S.A.M. 9329). Kruisvlei, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

Fig. 102.

Femora. (× $\frac{1}{6}$.) a. *Anteosaurus acutirostris*. S.A.M. 11977A. Dorsal view. b. *Anteosaurus acutirostris*. S.A.M. 11977A. Ventral view. c. *Anteosaurus acutirostris*. S.A.M. 11977A. Anterior view. d. *Anteosaurus* sp. S.A.M. 2753A. Ventral view. e. *Paranteosaurus primus*. S.A.M. 11485. Ventral view. f. *Anteosaurus* sp. S.A.M. 5614. Ventral view.

Anteosaurus lotzi (Broili and Schröder)

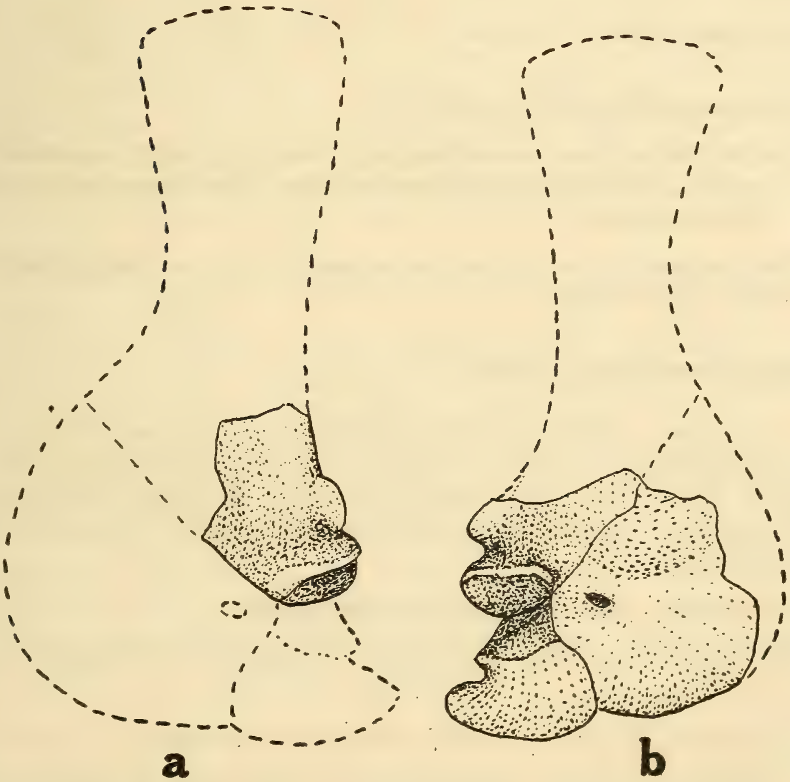
Alte Akademie. No. ?. Parts of an ilium, pubis and femur, associated with some skull pieces. Brakleegte, Beaufort West. High? *Tapinocephalus* zone. Coll. Schröder.

Little can be said about these fragments, but if the pubis is correctly determined and is as figured by Broili and Schröder, then this element is radically different from the pubes of other Deinocephalia.

Anteosaurus spp.

S.A.M. 2752. A partial distorted humerus and a coracoid, associated with a skull. Viviers Siding, Beaufort West. Mid *Tapinocephalus* zone. Coll. Haughton and Whaits.

Fig. 103.



Scapulo-coracoids. ($\times \frac{1}{6}$.) a. *Anteosaurus* sp. S.A.M. 5614. Lateral view. b. *Eccasaurus priscus*. S.A.M. 11597. Lateral view.

S.A.M. 2753A. Proximal and distal ends of a femur (Fig. 102d), associated with a skull fragment. Viviers Siding, Beaufort West. Mid *Tapinocephalus* zone. Coll. Haughton and Whaits.

S.A.M. 5614. Part of a scapula (Fig. 103a), an incomplete ilium (Fig. 104) and the proximal end of a femur (Fig. 102f), associated with two dentaries. Abrahamskraal, Prince Albert. Low *Tapinocephalus* zone. Coll. Haughton.

S.A.M. 7396. An isolated coracoid. Abrahamskraal, Prince Albert. Low *Tapinocephalus* zone. Coll. van der Byl.

S.A.M. 11887. An isolated coracoid. Vindraersfontein, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

Fig. 104.

Right ilium of *Anteosaurus* sp. S.A.M. 5614. (× ⅛.) Outer view.

Genus *Paranteosaurus* Boonstra

Paranteosaurus primus Boonstra

S.A.M. 11485. The proximal end of a femur (Fig. 102e), associated with a skull. Mynhardtskraal, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra.

This fragment shows no features by which it can be distinguished from the femur of *Anteosaurus*.

Genus *Micranteosaurus* Boonstra

The femur is slender and curved (length 210 mm.); the width over the external trochanter is 47 mm.; the shaft is long and narrow (diams. 28 × 18 mm.); a "twist" on the shaft causes the caput to be directed much dorsally; the ectepicondyle (and probably also the entepicondyle) is without any sheet-like expansion.

The fibula is very long (138 mm.) and slender.

The pes has the tarsal formula 2, 1, 5 and the phalangeal formula 2?, 3?, 3?, 4?, 2.

The radius (105 mm.) is much shorter than the fibula.

The manus has the carpal formula 3, 1, 5 and the phalangeal formula 3, 3, 4, 4?, 2.

Micranteosaurus parvus Boonstra

As I (4) have only recently described this form, the above generic diagnosis of the limbs is extracted from that account, which consult for the figures.

Type: S.A.M. 4323. A coracoid, radius, manus, femur, fibula and pes, associated with a snout. Commonage of Merweville, Beaufort West. Low *Tapinocephalus* zone. Coll. Haughton.

Genus *Eccasaurus* Broom

Notwithstanding its very distinctive humerus (which constitutes the type specimen) Broom (9) included this genus in the Tapinocephalia and later even referred a typical Tapinocephalian tooth to this genus.

Although Broom in his original description only mentions the humerus there is in the South African Museum collection, associated with the type humerus, some skull pieces, two imperfect and weathered femora, a flattened radius?, some vertebrae, the distal end of a fibula, some other fragments and a long slender simple pointed tooth, which is probably an incisor.

The generic characterisation below is based on the type supplemented by features determined from a second specimen (S.A.M. 11597).

In the scapula the tricipital tubercle is oval in outline and is situated 25 mm. above the edge of the glenoid; the other features of the scapulo-coracoid are as described above for the family. The humerus is 348-375 mm. long and the width of the shaft is 76-84 mm.; other features as for the family.

The only known ulna is crushed dorso-ventrally; the length is 260 mm.

The pelvis is unknown.

The femur is 355 mm. in length and fairly slender; the width over the external trochanter (120 mm.) is larger than in *Anteosaurus;* the epicondyles are not laterally expanded as thin flanges.

There is thus no doubt that *Eccasaurus* with its long pointed incisor, its humerus with the delto-pectoral crest very short, its slender femur, where the external trochanter is situated so far proximally and so little laterally, and in the referred specimen (referred because of the great similarity in the humeri) the distinctive tricipital tubercle on the scapula, cannot possibly be a Tapinocephalian but is in fact an Anteosaurian.

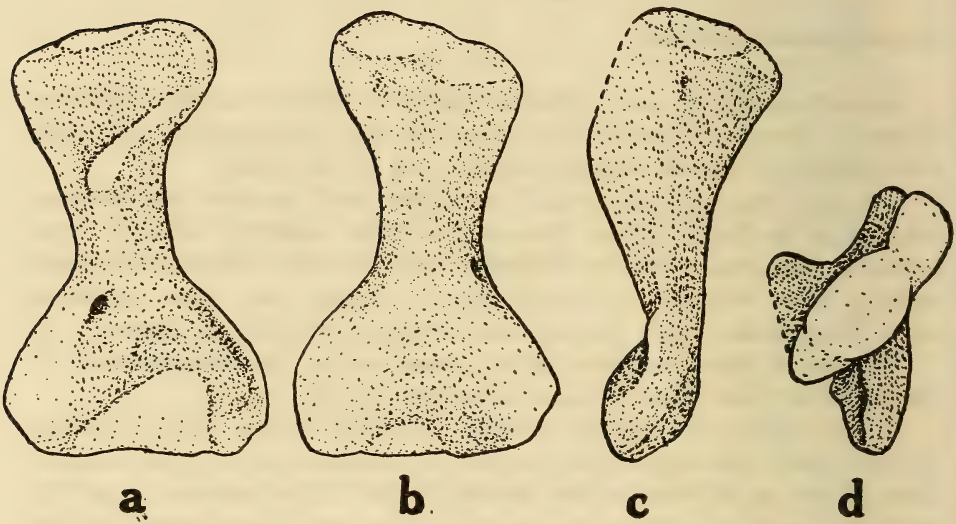
The tooth, which Broom has referred to *Eccasaurus,* does not belong to this genus but is typically Tapinocephalian.

Eccasaurus priscus Broom

The specific characters are as for the genus.

Type: S.A.M. 915. A good humerus (Fig. 105), two imperfect femora (Fig. 106), distal ends of the two fibulae (Fig. 107a) and a flattened ?radius, associated with parts of the skull. Sandvlakte, Prince Albert. Low? *Tapinocephalus* zone. Coll. Cairncross.

Fig. 105.



Humerus of *Eccasaurus priscus*. S.A.M. 915. (× ⅙.) a. Ventral view. b. Dorsal view. c. Anterior view. d. Proximal view.

Referred specimen:

S.A.M. 11597. Part of the right coracoscapula (Fig. 103b), an incomplete humerus and an ulna (Fig. 107b). Dikbome, Laingsburg. Low *Tapinocephalus* zone. Coll. Boonstra.

?*Anteosauridae Incertae Sedis*

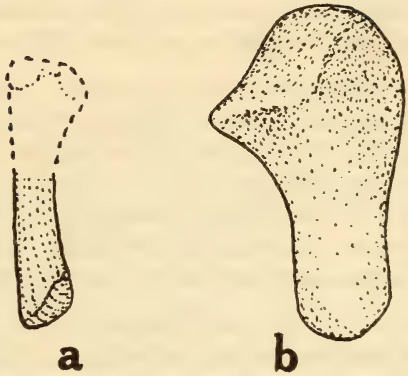
S.A.M. 11996. An isolated interclavicula (Fig. 108). Koedoeskop, Beaufort West. Mid *Tapinocephalus* zone. Coll. Boonstra.

This interclavicle is small, with a short, fairly narrow stem, and the anterior widely spatulate end is not curved up sharply. I am tentatively referring this bone to the Anteosauridae as it cannot belong to any of the other Deinocephalians, where this element has quite different features.

Fig. 106.

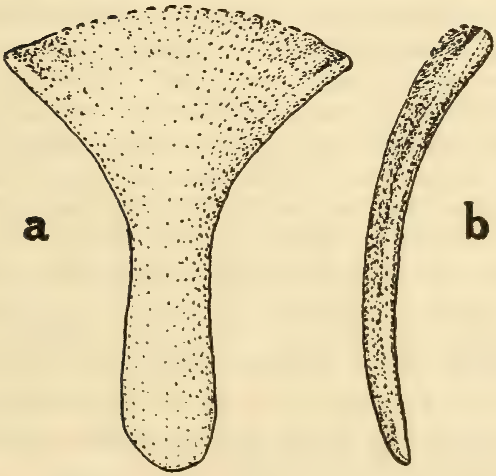
Femur of *Eccasaurus priscus*. S.A.M. 915. (× $\frac{1}{6}$.) a. Ventral view. b. Anterior view.

Fig. 107.



Eccasaurus priscus. (× $\frac{1}{6}$.) a. S.A.M. 915. Fibula in ventral view. b. S.A.M. 11597. Ulna in dorsal view.

Fig. 108.



Interclavicula of an ? Anteosaurid. S.A.M. 11996. (× $\frac{1}{6}$.) a. Ventral view. b. Lateral view.

Certain Palaeobiological Conclusions

From the above study it is abundantly clear that we still know very little about the girdles and limbs of the South African Deinocephalia.

Complete skeletons are unknown and moderately complete skeletons are extremely rare. In the herbivorous Tapinocephalia we have most specimens in which a fair amount of the skeleton has been found in association; in all about ten specimens (half of them of Moschopids) are known with a fair amount of the skeleton preserved in association. For the rest the specific and generic accounts are composite and based on a number of individuals, each with some part of the skeleton preserved, supplementing each other.

In the carnivorous Titanosuchia only two specimens have a fair amount of the skeleton of an individual animal preserved in association. In the Anteosauria only a few bones in all are known and in the Styracocephalia nothing whatever of the postcranial skeleton is known.

An inventory shows that parts of the girdles and limbs are known in 20 genera, and in 11 genera nothing at all is known of this part of the skeleton.

Now it is of interest to note that articulated partial skeletons have been more often found in the case of the Tapinocephalia than in the other infra-orders. This denotes a difference in the vicissitudes of entombment apparently largely due to differences in habitat. The two or three skeletons found in isolation were probably entombed in much the same manner as were the contemporary Pareiasaurs. In the two cases of mass-entombment of *Moschops* herds the conditions were different. Broom considered that the material of *Moschops* found by Whaits at Spitskop in the Moordenaarskaroo represents a herd of males, females and young. In the *Moschops*-material found by me at Kruisvlei in the Koup there are also males, females and juveniles, but here they were found together with remains of at least two individuals of the Anteosauria. There does not appear to be sufficient evidence for concluding that the two *Moschops*-finds represent herds over-whelmed by some catastrophy whilst peacefully feeding. It appears more probable that, living together in a certain suitable area, the remains were included in the sediment in a bed where deposition was taking place when death, not necessarily catastrophically or even simultaneously, overtook them. At Kruisvlei the bed in which the remains were found is not much more than about a foot thick and is a fairly fine argillaceous sandstone and the disposition of the various partial skeletons points to their having been transported by water for a short distance at least.

The other Tapinocephalian, and by far the majority of the Titanosuchian and Anteosaurian specimens, were found as isolated specimens consisting

of only a few bones not articulated but entombed quite near each other. The main reason for this scattering of the remains I believe to be due to the activities of carrion-eaters and the effects of water transport from higher to lower ground.

The above preliminary study of the locomotor apparatus in three of the infra-orders of the Deinocephalia has revealed three main types of locomotion. Without going deeply into this subject, at this stage, I can briefly indicate the broad differences that have become apparent.

In the Tapinocephalia the articulatory facets of the elbow-joint are weakly modelled and must have contained considerable cartilage. In addition the humeral condyles are situated much distally. This distal situation of the humeral condyles may indicate a more upright stance of the fore-limb when standing on firm ground. This is very probably the case in *Moschops* and its close relations, but in the Tapinocephalids and in many of the Struthiocephalids I am more inclined to think that the unfinished articulation is more indicative of a life spent much in water — but by no means as aquatic as the later Lystrosaurs. These reptiles living in the marshy parts of the Karroo basin, often wallowing in the water, but coming on firmer ground for part of their feeding would then, on death, be more likely to be entombed as fairly complete cadavers.

In the Titanosuchia the radial condyle is well modelled and the elbow-joint forms a much stronger and efficient hinge for terrestrial locomotion. But, the condyle being situated more on the ventral face of the humerus, this bone would in striding lie much more horizontally than in the Tapinocephalia. However, in the hind-limb, where the femoral condyles are placed much distally, the femur would be approaching a semi-upright position and the efficient joint with the tibia allows of the transmission of a powerful thrust by the hind-limb. Moreover, the muscle scars on all the elements of the stoutly built girdles and limb-bones are strong and indicate a muscular action much more powerful than in the Tapinocephalia and capable of the execution of sudden, rapid and forceful movements, which would be necessary for these carnivores. Thus the Titanosuchia, although having the chest slung fairly low between the fore-limbs, would be fairly active reptiles of prey, living chiefly on firm ground with little of the wallowing partaken of by the Tapinocephalia.

In the Anteosauria little is as yet known of the locomotor apparatus. The nature of the hip-joint and the structure of the femur seem to point to a crawling habit, showing, in some respects, much similarity to that of the modern crocodiles, but the dentition seems to indicate that they were possibly slinking carrion-eaters.

REFERENCES

1. Boonstra, L. D. A Note on the Synonymy of the two Deinocephalians, *Dinophoneus ingens* Broom and *Jonkeria pugnax* (Broom). S. Afr. Jour. Sci. 32, 329-331. 1935.
2. Boonstra, L. D. Some Features of the Cranial Morphology of the Tapinocephalid Deinocephalians. Bull. Am. Mus. Nat. Hist. 72, 75-98. 1936.
3. Boonstra, L. D. The Cranial Structure of the Titanosuchian: *Anteosaurus*. Ann. S. Afr. Mus. 42, 2, 108-148. 1954.
4. Boonstra, L. D. The Smallest Titanosuchid yet recovered from the Karroo. Ann. S. Afr. Mus. 42, 2, 149-156. 1954.
5. Boonstra, L. D. *Struthiocephalellus*: A New Deinocephalian. Ann. S. Afr. Mus. 42, 3, 180-184. 1955.
6. Broili, F. and Schröder, J. Ein Dinocephalen-Rest aus den unteren Beaufort-Schichten. Sitzb. Bay. Akad. Wiss. Sonderdruck, 93-114. 1935.
7. Broom, R. Notice of a new Fossil Reptile (*Scapanodon duplessisi*) from the Lower Karroo beds of Prince Albert, Cape Colony. Rec. Alb. Mus. 1, 3, 182-183. 1904.
8. Broom, R. Notice of some new Fossil Reptiles from the Karroo Beds of South Africa. Rec. Alb. Mus. 1, 5, 331-337. 1905.
9. Broom, R. Notice of some New South African Fossil Amphibians and Reptiles. Ann. S. Afr. Mus. 7, 3, 270-278. 1909.
10. Broom, R. Further Observations on South African Fossil Reptiles. Am. Mus. Jour. 14, 135-143. 1914.
11. Broom, R. On the Origin of Mammals. Phil. Trans. Roy. Soc. B.206, 1-48. 1914.
12. Broom, R. Permian, Triassic and Jurassic Reptiles of South Africa. Bull. Am. Mus. Nat. Hist. 25, 2, 105-164. 1915.
13. Broom, R. On *Tapinocephalus* and Two Other Dinocephalians. Ann. S. Afr. Mus. 22, 3, 427-438. 1928.
14. Broom, R. On the Carnivorous Mammal-like Reptiles of the Family Titanosuchidae. Ann. Transv. Mus. 13, 1, 9-36. 1929.
15. Broom, R. The Mammal-like Reptiles of South Africa. pp. 18-46. Witherby, 1932.
16. Byrne, F. A Preliminary Report on a New Mammal-like Reptile from the Permian of South Africa. Trans. Kans. Acad. Sci. 40, 221-231. 1940.
17. Gregory, W. K. and Camp, C. Studies in Comparative Myology and Osteology No. III. Bull. Am. Mus. Nat. Hist. 38, 15, 447-563. 1918.
18. Gregory, W. K. The Skeleton of *Moschops capensis* Broom, a Dinocephalian Reptile from the Permian of South Africa. Bull. Am. Mus. Nat. Hist. 56, 3, 179-251. 1926.
19. Haughton, S. H. On a Skull of *Tapinocephalus atherstonei*, Owen. Ann. S. Afr. Mus. 12, 1, 40-42. 1915.
20. Haughton, S. H., in Report of the South African Museum for 1915, p. 4. 1916.
21. Huene, F. von. Beitrag zur Kenntnis der Fauna der südafrikanischen Karroo-formation. Geol. Pal. Abh. 18, 3, 159-227. 1931.
22. Lydekker, R. Catalogue of the Fossil Reptilia and Amphabia in the British Museum (Natural History) IV, 81-98. 1890.
23. Owen, R. Descriptive and Illustrated Catalogue of the Fossil Reptilia of South Africa in the Collection of the British Museum, 1-86. 1876.
24. Owen, R. Description of Parts of the Skeleton of an Anomodont Reptile (*Platy-podosaurus robustus*, Ow.) from the Trias of Graaff-Reinet, S. Africa. Quart. Jour. Geol. Soc. 36, 414-425. 1880.
25. Romer, A. S. The Locomotor Apparatus of Certain Primitive and Mammal-like Reptiles. Bull. Am. Mus. Nat. Hist. 46, 10, 517-606. 1922.
26. Rossouw, P. J. en de Villiers, J. Die Geologie van die Gebied Merweville, Kaapprovinsie. Toel. Blad. 198. Geol. Opname, Unie S.Afr., 1-71. 1952.
27. Seeley, H. G. Researches on the Structure, Organisation and Classification of the Fossil Reptilia. II. On *Pareiasaurus bombidens* (Owen), and the Significance of its Affinities to Amphibians, Reptiles and Mammals. Phil. Trans. Roy. Soc. 179, B. 59-109. 1888.
28. Seeley, H. G. Researches on the Structure, Organisation and Classification of the Fossil Reptilia. VI. On the Anomodont Reptilia and their Allies. Phil. Trans. Roy. Soc. 180, B. 215-296. 1889.
29. Watson, D. M. S. The Deinocephalia, an Order of Mammal-like Reptiles. Proc. Zool. Soc., 749-786. 1914.

PLATE XXV.—Photograph of a life-size model of *Struthiocephalus whaitsi* as exhibited in a habitat group in the South African Museum. Modelled by the author.

Photo: Nasionale Pers Bpk.

ANNALS

OF THE

SOUTH AFRICAN MUSEUM

VOLUME XLII

Descriptions of the Palaeontological Material acquired by the South African Museum and the Geological Survey of South Africa.

PART IV, *containing:—*

ISSUED MARCH 1956. *PRICE 10s. od.*

PRINTED FOR THE

TRUSTEES OF THE SOUTH AFRICAN MUSEUM

AND FOR THE

GEOLOGICAL SURVEY OF SOUTH AFRICA

BY THE NATIONAL COMMERCIAL PRINTERS LIMITED

JAN VAN RIEBEECK STREET, ELSIES RIVER

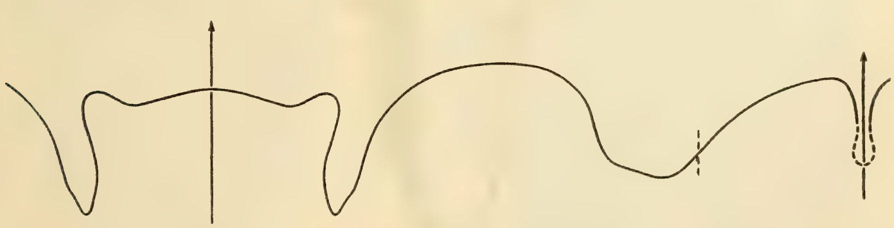
15. *Tertiary Nautiloids dredged near Cape of Good Hope.* By A. K. MILLER and W. M. FURNISH, State University of Iowa, Iowa City, Iowa.

(With Plate XXVI and 2 text-figures.)

Four Aturias from collections in the South African Museum at Cape Town were recently sent to us on loan by Dr. Sidney H. Haughton, formerly of the Union of South Africa Geological Survey. These specimens were secured early in 1938 by Captain J. T. R. Gibson, skipper of a trawler belonging to Messrs. Irwin and Johnson; he dredged them from a depth of 160 to 170 fathoms just west of Cape of Good Hope, between Slangkop Lighthouse and Cape Point. A single species is represented by the four specimens, which are internal molds composed of phosphate rock. Dr. Haughton has informed us that similarly preserved lamellibranchs, gasteropods and some mammalian remains were found associated.*

Representatives of *Aturia,* though almost invariably rare, are of very widespread occurrence in the marine Tertiary. They range from the Eocene to the Miocene, inclusive, and may have been found in slightly older strata. In the Atlantic-Gulf coastal region of North America, where Tertiary deposits are well developed and have been studied extensively, Aturias do not occur below the base of the Eocene, and they are known from only one locality in the Miocene. However, in westernmost North America, South America, and Europe they seem to be less rare in the Miocene. After studying specimens from many widely separated localities in various parts of the world, we are convinced that typical representatives of the genus have a long range in the Tertiary. Therefore, we can not be certain as to the precise age of the specimens under consideration.

FIG. 1.—*Aturia lotzi* Böhm, Suture.



*) The first record in print of the occurrence of *Aturia* in the phosphatic-glauconitic deposit off the Cape of Good Hope appears to be in L. Cayeux: *The Phosphatic Nodules of the Agulhas Bank.* Ann. S. Afr. Mus. XXXI, p. 133. 1934. [Ed.]

The more diagnostic features of these Cape of Good Hope nautiloids are elucidated by the accompanying illustrations. In general physiognomy, this form is reminiscent of similar-sized Aturias from the Americas. Because of the width and shape of the umbilical lobe of the sutures, it can be said to belong in a group typified by *Aturia angustata* (Conrad) of the Oligocene and Miocene of the North American Pacific coastal region. The nearest geographic occurrence of the genus is that of *A. lotzi* Böhm at Bogenfels, some 500 miles north. Insofar as we can tell from the published information in regard to the type specimens of that species, they are conspecific with those we are studying. All of them came from a sandstone which carries a fauna generally identified as Miocene.

Each of the four specimens under consideration represents a different portion of the phragmocone, and it is possible that all are parts of a single large individual, which (including the body chamber) had a diameter of 250 mm., or more. In every case, the surface is smooth and polished but, nevertheless, bears serpuloid worm tubes, even on the exposed septa. Clearly, the pieces lay loose on the bottom of the sea and were dissociated.

It should perhaps be stated that Aturias are known from latitudes as far north and south as 55 or 60 degrees. Specimens have been collected from Tierra del Fuego, Tasmania, and New Zealand. Therefore, their discovery near southernmost Africa is not surprising.

REFERENCE

Miller, A. K.: Tertiary nautiloids of west-coastal Africa: Mus. Congo Belge, Ann., Sér. in 8°, Sci. Géol., vol. 8, pp. 1-88, pls. 1-31. 1951.

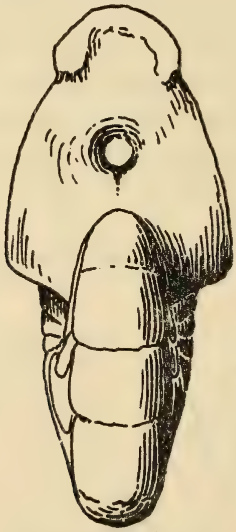


Fig. 2.—*Aturia lotzi* Böhm. Drawing traced from a photograph to show position of siphuncle. This excellently preserved specimen was obtained by the South African Museum from off Cape Columbine, Saldanha Bay area, after this paper had been received from the authors, and has not been seen by them. Natural size. [Ed.].

PLATE XXVI. FIGS. 1-4.—*Aturia lotzi* Böhm. Two views, naturel size, of two smaller specimens dredged near Cape of Good Hope — photographs retouched by Mr. Frederick Leach. The suture drawing (text-figure 1) is based on the fragment portrayed by figures 1 & 2.

16. *Phosphatic-Glauconitic Deposits off the West Coast of South Africa.* By S. H. Haughton, D.Sc., F.G.S.

From time to time there have come into the possession of the South African Museum in Cape Town various phosphatised invertebrate and vertebrate remains and phosphatic nodules that have been dredged off the west of the Cape Peninsula at depths of over 100 fathoms. Most of those which were received after 1930 were confided to me for examination; but pressure of other work prevented an attempt at systematic study of this very interesting material.

In the Annual Report of the South African Museum for 1905 (p. 10), Dr. J. D. F. Gilchrist, who was in charge of the collections made during the dredging and collecting expeditions of the Government research vessel "Pieter Faure" stated: "The working out of the fossil remains in a series of deep sea deposits has been undertaken by Dr. Broom." There is no record of this work having been completed; but in a letter to Dr. Gilchrist, dated 20th August, 1905, from Stellenbosch Broom referred to a "fragment of a Nautiloid shell" which he had no hesitation in identifying as "*Aturia aturi*, a Miocene Nautiloid found in Miocene of France, Italy, Malta and Australia". In the same letter he referred to a "*Terebratula*" and to "whales". The *Aturia* specimen is not in the South African Museum collection; the other material referred to by Broom has not been definitely located.

Early in 1938, Capt. J. T. R. Gibson, skipper of a trawler owned by Messrs. Irvin and Johnson, deposited at the Museum some material which he had dredged from a depth of 160-170 fathoms between Cape Point and Slangkop Lighthouse. This included internal casts of a *Xenophora*-like shell and four fragments of an *Aturia*, all phosphatised. The *Aturia* seemed to be indistinguishable specifically from *Aturia lotzi*, the type of which came from Tertiary beds near Bogenfels in South West Africa. In the latter half of 1953 these four fragments were sent for examination to Dr. A. K. Miller of the State University of Iowa whose publication on "Tertiary Nautiloids of West-Coastal Africa" (*Ann. Mus. Congo Belge, Sci. Géol.*, Vol. 8, 1951) is the authoritative work on the subject. Dr. Miller confirmed their attribution to *A. lotzi* Böhm, and is publishing a separate note on them.

In the Annual Reports of the South African Museum for 1948, 1950, 1952, and 1953 Dr. K. H. Barnard made brief mention of further phosphatised

material obtained from Capt. Gibson, the Fisheries Survey, and from a depth of approximately 200 fathoms off Cape Columbine, the last presented by the Department of Geography of the University of Cape Town. Cape Columbine lies to the north of Saldanha Bay, forming the southern headline of Klein Paternoster bay.

The petrological and mineralogical characteristics of phosphatic material dredged by the S.S. "Pieter Faure" from the Agulhas Bank, together with an account of the probable geological history, were considered in detail by L. Cayeux (*Ann. S.Afr. Mus.*, XXXI, 1934, p. 108). Some of the material collected by Capt. Gibson was studied in the Geological Survey Laboratories by Dr. J. E. de Villiers, now Professor of Geology in the University of the Orange Free State, Bloemfontein.

Dr. de Villiers recognised two major varieties of phosphate rock. One is a conglomeratic type, composed of irregular nodules set in a cement; the other is more homogeneous and similar to the "cement" of the conglomeratic type. He reported that "the nodules consist of yellow-brown, amorphous-appearing phosphate which for the most part is crowded with calcareous organic remains. Angular mineral fragments (quartz, albite, orthoclase, labradorite, zircon, garnet, tourmaline and muscovite) and small, rounded grains of glauconite are also present. X-ray examination of the phosphate showed it to have a pattern identical with that of francolite from the Richtersveld. In a few instances it was found that the nodules had been glauconitised at or near the contact with the matrix; the glauconitisation took place before cementation of the nodules — uncemented nodules occur which have a rim of glauconite."

"The cementing material of the matrix is collophanite. Calcareous inclusions and tests of foraminifera are more rare than in the nodules, and quartz and round glauconite grains are more plentiful. The fragments and grains of these two minerals are larger in the matrix than in the nodules and the ratio of glauconite to quartz is about 4 : 1. Tiny dust-like specks of iron oxide and perhaps carbon are irregularly distributed and cause the colour to vary from light to darker yellow-brown" (De Villiers).

The "conglomeratic" material, therefore, has had a composite geological history. The "nodules", which are often angular or semi-angular and of irregular shape, may be pieces of an originally calcareous sediment containing fragments of bone, shells, and foraminiferal tests which suffered a degree of phosphatisation before fragmentation. The fragments which now form the nodules became embedded in a glauconite sand containing some foraminifera together with the grains of quartz and other terrigenous material which in its turn became phosphatised and cemented, forming a phosphorite. The fragments as now dredged are irregular in shape. In the conglomeratic samples, the older fragments exist in juxtaposition to the newer cement at the surface

of the specimens, sometimes protruding. Many have a veneer of glauconite; many are partially encrusted with calcareous material, serpulid tubes, and sponge spicules. In cavities in the irregular dredged fragments there was sometimes found sand consisting of abundant grains of quartz and felspar, some rounded glauconite grains, and organic material consisting of numerous sponge fragments, calcite plates minutely perforated, a few globigerina tests, and plates of chitin. This, and the sand found in phosphatised ear-bones of whales, is the youngest material in the collection.

Cayeux (*Ann. S. Afr. Mus.*, XXXI, 1934, p. 124) in his description of a "nodule formed of two differing rocks" was obviously dealing with material similar to the "conglomeratic type" of de Villiers, although his specimen was of such a nature that he was unable to say that one rock served as a matrix to the other. The lighter-coloured rock he considered to be a phosphatised "bryozoan foraminiferal limestone", the other a phosphatised greensand. He pointed out, however, that these two rock types must have been formed under differing bathymetric conditions and formulated the idea of *remanié* material from a deposit formed originally at a greater depth being incorporated in shallower water greensands.

The four specimens assigned by Miller to *Aturia lotzi* are composed lithologically of the same kind of material as forms the "nodules" in the "conglomeratic type". The Bogenfels specimens of *A. Lotzi* described by Böhm were obtained from a marly sandstone of terrigenous origin which now stands 140-160 m. above the sea, considered by him (1926) to be of Middle and Upper Eocene age. The general nature of the succession of beds in the Bogenfels area shows that they are near-shore deposits; uplift of the order of 400-500 feet is thus indicated for them. The fragments studied by Miller must have been deposited therefore in an environment different from those found in the Bogenfels beds, the former at a greater depth below sea-level and farther from the shore than the latter.

More recently two more specimens of *Aturia lotzi* were acquired by the South African Museum. They had been trawled from the Saldanha Bay-Cape Columbine area of the west coast, but the depth and actual position of the find are unknown. The discovery area is well to the north of that from which Capt. Gibson obtained the four specimens examined by Miller, and therefore nearer to Bogenfels, but the matrix is said by Dr. Barnard to be like that of the others.

Among the material dredged off Cape Columbine were nodules containing more or less fragmentary lamellibranchs and brachiopods. These were sent for study to Dr. Helen Muir-Wood of the Department of Geology of the British Museum (Natural History) who, in turn, passed the lamellibranchs on to her colleague Dr. L. R. Cox. Both these experts have been good enough to favour me with their comments on the material examined.

Dr. Muir-Wood stated:—

"I have looked at the four brachiopods dredged off Cape Columbine, but can give you no specific determinations or any definite information, about their age. They are not comparable with anything from South Africa, and we have no specimens from other areas that are altogether similar. They could be Miocene in age as suggested by Dr. Cox, and the two Terebratulids are externally rather like specimens of *'Terebratula' miocenica* Michelotti from the Miocene of Italy. I have no idea whether the African forms are actually related to the Italian species, since the internal characters of both are unknown.

"The larger of the two Terebratulinids is probably new. I have compared it with *Cancellothyris* which does occur in the Miocene, but do not think it belongs to this genus. The smaller specimen will have to be compared with the Recent species *Terebratulina retusa* (Linn.). This species, usually quoted as *T. caputserpentis* (Linn.) appears frequently in fossil lists of species from the Miocene or Pliocene.

"The Tertiary brachiopods are in great need of revision and it is difficult at present to give specific determinations."

Dr. L. R. Cox reported on the molluscan fossils as follows:—

"They have nothing in common with the assemblage described by Böhm and Weissermel from the Bogenfels diamond fields and do not, in fact, link up at all with any fossels hitherto described from Africa. They may be recorded as follows:—

"*Ostrea (Pycnodonta)* cf. *brogniarti* Bronn. This is the Gryphaea-like oyster, of which there are several specimens, some with a very spongy texture. *O. brogniarti,* which is scarcely distinguishable from the Cretaceous *O. vesicularis* Lamarck, is widespread in the Eocene of the Tethyan province, persisting into the Oligocene of several Mediteranean countries, and being last met with in the Lower Miocene (Aquitanian) of N. Italy. Of its recorded localities, the nearest to S. Africa is the Belgian Congo, where it occurs in the Paleocene. It could conceivably have survived to the Miocene off S.W. Africa.

"*Pecten* sp.nov. This species, of which there are two or three specimens, has the right valve strongly convex and the left valve almost flat, and therefore belongs to *Pecten s. str.* The left valve has fine, evenly spaced concentric threads, crossing ribs and intervals. This species belongs to a group well represented in the Oligocene and Neogene of the Mediterranean and N. W. Indian Ocean areas, but absent in the Eocene except in California. It does not appear to be identical with any described species.

"*Chlamys* spp. indet. There are three ill-preserved specimens of equivalve ribbed Pectinids, probably belonging to two different species. The details

of the ornament cannot be observed and the specimens throw no light on the geological age of the deposit.

"*Conus* sp. indet. One ill-preserved internal mould.

"*Cadulus* sp. indet. One internal mould.

"The material is too limited and ill-preserved to allow the age to be established definitely. A lower Miocene age would, however, be compatible with the presence of oysters indistinguishable from *O. brogniarti* Bronn associated with specimens of *Pecten* s. str., a group which, although found in the Oligocene, does not become abundant until the lower Miocene. The moulds of worm tubes and of two species of corals do not assist in the determination of age."

Apart from the material submitted for examination to overseas specialists, there remains in the collections of the South African Museum a considerable number of phosphatised specimens obtained from dredging off the west coast of the Cape Peninsula at various times since the S.S. "Pieter Faure" was used as a governmental research ship under Dr. J. D. F. Gilchrist. These hav been examined by Dr. K. H. Barnard, who has supplied the following identifications for purposes of record:—

MAMMALIA

Otoliths of *Balaena* (Right Whale), *Balaenoptera* (Finner Whale), *Megaptera* (Humback Whale). Portion of skull of unidentified cetacean (S.A.M. Reg. No. 19475).

Anterior portions of skulls of *Mesoplodon* spp.

(a) With maxillary and premaxillary foramina on same transverse line (S.A.M. Reg. Nos. 19473 and 19934). Cf. *M. europaeus*, *M. bidens*, *M. layardii*.

(b) One with premaxilliary foramina posterior to maxillary foramina (S.A.M. Reg. No. 19930). Cf. *M. densirostris*, *M. grayi*, *M. australis*.

Anterior portion of skull of *? Ziphius*, with gibbous maxillaries (S.A.M. Reg. No. 19942).

Hind portions of left mandible with 7 tooth-sockets of *Orca* sp.

PISCES

Carcharodon sp. — teeth.
Carcharias sp. — teeth.
Isurus or *Lamna* sp. — teeth.
Histiophorus sp. — portion of rostrum.

GASTROPODA. (Internal casts.)

Xenophora sp.
Conus (?) sp.
Cf. *Pleurotoma* sp.
Cf. *Pusionella* sp.
Fusus (?) sp.
Natica sp.

LAMELLIBRANCHIA. (Internal casts.)

Cuspidaria sp.
Venerid (?).

SCAPHOPODA. (Internal casts.)

Dentalium sp.

Most, if not all, of this material would appear to be associated with the later glauconitic greensand type of deposit. The impossibility of specific identification of these various forms renders comparison with other described faunas hazardous; and clearly further attention should be paid to the collection of additional material and to intensive study of a fossil assemblage that seemingly is contained in rocks of at least two differing ages. Study of the foraminifera, which occur abundantly in the "nodules" and more sparsely in the "cement" should be of assistance. Such evidence as has been yielded by the macro-fossils, however, suggests that the foraminiferal "nodular" part of the dredged material is of Miocene (and even of Lower Miocene) age and that it may represent a somewhat deeper-water facies of the Bogenfels beds which carry *Aturia lotzi*.

17. *Fossil Carnivora from Hopefield.* By R. F. Ewer, Zoology Department, Rhodes University, Grahamstown, and R. Singer, Anatomy Department, University of Cape Town.

(With Plates XXVII-XXXII and 1 text-figure.)

I. Introduction

The history and general appearance of the fossil site on the farm "Elandsfontein", 10 miles from Hopefield — a village 90 miles north of Cape Town — has already been described in a fairly detailed manner (Drennan, 1954; Singer, 1954). The movement of the exposed crescentic sand-dunes situated in the scrub-covered bushveld has uncovered calcareous floors from which a wealth of fossil material has been recovered by a research team of the University of Cape Town. Besides the human cranial fragments (see above publications, and also Drennan and Singer, 1955) and stone implements of the final phases of the South African hand-axe culture and of the Still Bay culture, many species of extant and extinct mammals have already been identified — Equidae, *Homoioceras (?Bubalus)* sp., *Palaeoloxodon* cf. *antiquus recki, Ceratotherium* and *Diceros, Giraffidae (?Sivatherium), Hippopotamus amphibius* and *Mesochoerus lategani* (Singer and Keen, 1955), and numerous types of antelopes (eland, wildebeest, lechwe, etc.). A small number of fossilized tortoise carapace fragments, shells of *Succinea,* land snails *(Trigonephrus globulus),* and a cranial fragment of a scaly anteater, have also been recognized. Fossil Carnivora are not abundant at Hopefield, but the remains which have been recovered to date show that the fauna included a viverrid, two hyaenids, a small felid, a *Lycaon,* a jackal and a mustelid. The material is described in detail below.

II. Descriptions

1. Family *Viverridae*

Specimen E.C.7: the top of a braincase with the greater part of the occiput.

In size and general conformation the specimen closely resembles *Herpestes ichneumon* (Linn.), but in view of its incompleteness no detailed comparisons are possible.

2. Family *Hyaenidae*

The Hyaenid remains represent two species, one of which is a *Hyaena*, closely resesmbling the living *H. brunnea*, and the other a large *Crocuta*.

(i) *Hyaena brunnea* Thunb.

Specimen E.C.2: right mandibular ramus, lacking the coronoid process and with I_1 and I_2 broken off; all the other teeth are present in a good state of preservation and showing only slight wear.

Specimen E.C.3: portion of left mandible bearing the canine, P_2, P_3 lacking its anterior end, P_4 and slightly damaged M_1. This almost certainly belongs to the same individual as E.C.2.

Specimen E.C.4: maxillary fragment with P^3, P^4 and M^1. These teeth occlude perfectly with those of E.C.3, and there is no doubt that they belong to the same individual.

Specimen E.C.6: maxillary fragment with P^3 and the anterior roots of P^4.

Specimen E.C.11: maxillary fragment with milk carnassiail and Mm^4.

These specimens do not show any important differences from the living *Hyaena brunnea* Thunb. The measurements of the teeth are given below and compared with the corresponding values found for a sample of 15 specimens (13 measurements for mandibles) of the living brown hyaena (table 1). For each measurement of the latter the mean and standard deviation are given. From the ratio of the difference between the fossil measurement and the mean to the standard deviation can be found P, the probability of a specimen from the same population as the living specimens having a measurement as divergent as that of the fossil.

In the dimensions of the upper teeth none of the fossils differs significantly from the living species. In the case of teeth from the mandibles some slight differences are apparent: the carnassials and P_3 are slightly smaller, and P_4 is slightly narrower both absolutely and relatively. The smaller lower carnassial and slightly lesser development of the crushing specialisations of P_3 and P_4, as reflected in their slightly smaller widths, are points in which the fossil specimens appear to be a little more primitive than their living counterparts. The differences are so slight, however, that it has not been considered necessary to place the fossil specimens in a distinct subspecies.

A subspecies of *Hyaena brunnea*, *H. brunnea dispar*, has been described by Ewer (1955) from Swartkrans. In this subspecies P^4 is slightly shorter than in the living form and P^3 is more primitive, the posterior cusp being rather large and the anterior ridge situated less internally. The Hopefield specimens do not show these characteristics. The only point of resemblance between the two is that P_3 in each case is shorter than in the living form, but

in the Hopefield specimen the tooth is smaller in both its linear dimensions, whereas in the *dispar* subspecies the width is not significantly different from that of the living form. There is thus little justification for including the Hopefield specimens in the *dispar* subspecies.

TABLE 1.

Measurements of fossil *Hyaena brunnea* compared with those of a sample of 13 mandibles and 15 skulls of living *H. brunnea.* For the latter the mean and its standard deviation are given. $\frac{d}{\sigma}$ is the difference between the fossil measurement and the mean divided by the standard deviation of the latter. P gives the probability of a measurement as divergent as that of the fossil specimen being found in the population from which the sample of living *H. brunnea* was drawn. Values marked with an asterisk are statistically significant.

All measurements, in this and the succeeding tables, are given in millimetres.

	Specimen No.		Living *H. brunnea*		$\frac{d}{\sigma}$	P
	E.C. 2	E.C. 3	Mean	S.D.		
I_3 length	7·1		6·60	·56	·89	>·05
breadth	7·2		7·56	·41	·88	>·05
$\bar{C}$ length	15·3	15·2	17·16	1·14	1·86	>·05
breadth	12·2	11·9	13·35	·84	1·05	>·05
P_2 length	14·8	15·1	15·55	·50	1·50	>·05
breadth	10·0	10·5	11·03	·50	2·03	<·05>·04
length : breadth ratio	1·48	1·44	1·41	·06	1·16	>·05
P_3 length	19·6		21·17	·40	3·70	<·0004*
breadth	12·7	12·7	14·40	·60	2·83	≏·005*
length : breadth ratio	1·54		1·47	·06	1·20	>·05
P_4 length	23·2	23·1	23·59	·56	·88	>·05
breadth	12·4	12·4	13·80	·51	2·75	<·01>·005*
length : breadth ratio	1·87	1·86	1·71	·06	2·67	<·01>·005*
M_1 length	22·4	22·4	24·56	·89	2·43	<·02>·012*
breadth	11·3	11·4	12·61	·43	3·05	<·003>·001*
	E.C. 4	E.C. 6				
P^3 length	23·1	22·2	22·88	·63	1·08	>·05
breadth	15·9	15·9	15·98	·70	·11	>·05
length : breadth ratio	1·45	1·40	1·43	·05	·06	>·05
P^4 length	35·8		35·31	1·08	·45	>·05
breadth	21·1		21·48	·68	·56	>·05
M^1 length	6·0		5·62	·38	1·00	>·05
breadth	14·0		13·07	·87	1·07	>·05

(ii) *Crocuta spelaea* (Goldf.).

Specimen E.C.1: posterior half of skull, broken off at about the level of the post-orbital constriction. The zygomata are missing and the auditory bullae broken, but otherwise the specimen is almost perfect (Pls. XXVII-XXIX).

Specimen E.C.9: mandibular fragment with much damaged P_2, P_3, P_4 and the alveoli of M_1.

Specimen E.C.8: mandibular fragment with the anterior two thirds of M_1 (Pls. XXX, XXXI).

Specimen E.C.5: maxillary fragment with P^3 and damaged P^4 (Pls. XXX, XXXI).

The skull is large and heavily built, the occiput high and narrow, and very distinctly "shouldered" (see Pl. XXVIII). The lambdoid and sagittal crests are well developed, and the latter is very high posteriorly. The conformation of this region is very similar to that of a skull of *Crocuta spelaea* from Sundwig in the British Museum of Natural History (No. 28558) and an occipital fragment (M. 4570) from Torbryan Caves also shows similar development of the crests.

Goldfuss (1821) notes as a characteristic of *Crocuta spelaea* the large development of the post-glenoid process. This is not at all an easy character to assess or to measure, particularly since in fossil material the tip of the process is commonly slightly damaged. From an examination of the *C. spelaea* material in the British Museum of Natural History it appears that, apart from its size, the post-glenoid process of *C. spelaea* differs from that of *C. crocuta* (Erxl.) in its orientation. In *C. spelaea* the process lies almost in the transverse plane of the skull, whereas in *C. crocuta* it slopes distinctly forward from its outer to its inner end. In specimen E.C. 1 the process is orientated as in *C. spelaea* (Pl. XXIX).

Unfortunately both the carnassials are damaged posteriorly, but the presence of posterior roots makes it possible to restore the missing portions with a fair degree of accuracy, and at least to determine a minimum length. In specimen E.C. 5 the palate is somewhat damaged at the posterior end of P^4, and it is therefore impossible to be quite certain that M^1 was absent, but clearly if present at all it can only have been very small. The upper carnassial possesses the long metacone and relatively short parastyle characteristic of advanced Crocutas, but the protocone does not slope forward as much as is usual in *C. spelaea*. The lower carnassial, apart from its large size, is remarkable only for the structure of the anterior cingulum. This forms a sharp shelf-like excrescence round the antero-external margin of the tooth extending for just over 2 mm. and then ceasing abruptly at either end. Since the posterior portion of the tooth is missing the characters of the talonid are unknown.

The premolars do not provide any distinctive characters but closely resemble those of *Crocuta crocuta*, except for their larger size. The posterior part of P_2 is missing, but the posterior root is very broad: P_2 in *C. spelaea* is commonly very wide at the posterior end.

The measurements of the specimens are given below, compared, in the same way as before, with the corresponding figures for *C. spelaea* (table 2). The only points of difference are that the premolars are a trifle narrower in the Hopefield than in the European specimens. In this character the Hopefield specimens resemble the *capensis* subspecies of *C. spelaea* described by Broom (1939) (see also Ewer 1954) from Kromdraai. *C. spelaea capensis*, however, differs from typical *C. spelaea* also in the large and almost square M^1 and in the very long P^3, neither of which characters is shown by the Hopefield specimens. In addition the protocone of P^4 in *C. spelaea capensis* is large and slopes forwards very considerably. The general narrowness of the premolars is a primitive character, and cannot, by itself, be taken to indicate any particular close relationship of the Hopefield specimens to *C. spelaea capensis*. The former are best regarded as closely resembling the typical European *C. spelaea*, differing only in the slightly more primitive character of the premolars. This difference does not seem of sufficient importance to

TABLE 2.

Measurements of Hopefield specimens of *Crocuta spelaea*. The dimensions of the teeth are compared with those of a sample of *C. spelaea* from various European localities: the figure in brackets after the mean for the latter gives the number of specimens on which the mean is based. Other symbols as before.

Specimen E.C. 1.
Maximum vertical height of sagittal crest above upper edge of foramen magnum 81·6 mm.
Maximum vertical height of external occipital protuberance above foramen magnum 55·0 mm.
Maximum width across occipital condyles 47·0 mm.
Maximum width of skull (intersquamosal) 95·0 mm.
Maximum width across mandibular fossae ca. 124·0 mm.

		European sample		$\frac{d}{\sigma}$	P
		Mean	S.D.		
Specimen E.C. 9					
P_2 length	ca. 17·5	16·9 (31)	·85	·71	>·05
P_3 length	22·2	22·7 (33)	·78	·64	>·05
breadth	14·6	16·5	·93	2·04	≃·04
length : breadth ratio	1·52	1·38	·054	2·59	≃·01*
P_4 length	24·5	23·5 (32)	1·13	·89	>·05
breadth	13·5	14·9	·87	1·61	>·05
length : breadth ratio	1·81	1·58	·088	2·61	≃·01*
Specimen E.C. 8					
M_1 length	ca. 30·5	32·4 (26)	1·33	1·43	>·05
breadth	12·8	13·7	·73	1·23	>·05
Specimen E.C. 5					
P^3 length	24·3	24·1 (19)	1·34	·15	>·05
breadth	16·6	17·9	1·17	1·11	>·05
length : breadth ratio	1·46	1·35	·52	2·11	<·04>·03
P^4 length	ca. 40	40·9 (27)	·92	·98	>·05
breadth	ca. 21	22·5	1·22	1·23	>·05

warrant the erection of a new subspecies for the Hopefield specimens, but should be borne in mind in considering the probable age of the deposit.

3. Family *Felidae*

(?) *Leptailurus serval* (Schreber).

Specimens E.C.15, E.C.17: mandibular rami, incomplete anteriorly and posteriorly, bearing P_3 P_4 and M_1.

Specimen E.C.16: portion of mandibular ramus with P_4 and M_1.

The specimens all belong to a small felid, and the teeth do not show any peculiar characters. A set of skulls is not available to us for detailed comparison, but, judging from the measurements given by Roberts (1951), the specimens are a trifle too large to belong to the Cape wild cat, *Felis cafra* Desmarest, and fall within the range of *Leptailurus serval* (Schreber), to which species they are tentatively referred.

TABLE 3.

Measurements of fossil specimens of *Leptailurus serval.*

	Specimen No.		
	E.C. 15	E.C. 16	E.C. 17
Depth of mandible between P_4 and M_1	13·5	15·2	ca. 15·5
P_1 length	8·7		7·5
breadth	4·8		3·9
P_3 length	10·5	10·7	9·7
breadth	5·8	5·1	5·1
M_4 length	12·3	11·4	11·5
breadth	6·2	4·9	5·5

4. Family *Canidae*

(i) *Lycaon pictus* (Temm.) n. subsp. *magnus*.

Diagnosis:

A subspecies of *Lycaon* differing from the extant form in the greater length of the mandible, larger lower canines and incisors and longer but relatively narrower lower premolars.

Specimen E.C.13: portion of left mandibular ramus, incomplete below and bearing P_1 to P_4 and the anterior root of M_1. (Pls. XXX, XXXI.)

Specimen E.C.121: right mandibular fragment bearing I_2, I_3 and $\overline{C}$.

Specimen E.C.30: isolated damaged right M_1.

All three specimens show moderate wear and are in a very similar state of preservation: it is probable that they belong to a single individual. Apart

from their distinctly greater length the teeth differ in no way from those of the living *Lycaon pictus* (Temminck). The measurements are given below, compared as before with those of the extant species. It will be seen that the fossil jaw is considerably longer than that of the extant species and that the teeth differ significantly from those of the latter in the following points: the premolars are considerably longer, but not much broader; the canine and I_3 are significantly larger in both dimensions while the significance of the slightly greater breadth of I_2 is less certain. It is considered that these differences are sufficiently clear cut to warrant placing the fossil specimens in a distant subspecies.

Wells & Cooke (1942) record from Vlakkraal a damaged M_1 and a worn I_3; the latter is said to be "a little larger than any specimen of this genus actually axamined." It seems not improbable that this belongs to the same subspecies as the Hopefield material.

TABLE 4.

Dimensions of teeth of fossil *Lycaon* compared with those of a sample of 1 extant *Lycaon pictus*. Symbols as before.

	Specimen No.		Extant *L. pictus*		$\frac{d}{\sigma}$	P
	E.C. 12	E.C.13	Mean	S.D.		
Length from back of P_4 to front of P_1		52·8	40·7	1·79	6·76	<·0004*
I_2 length	5·5		4·48	·57	·04	>·05
breadth	5·6		4·71	·39	2·29	<·03>·02
I_3 length	7·6		6·03	·47	3·34	<·001>·0004*
breadth	6·5		5·66	·30	2·80	≏·005*
$\bar{C}$ length	13·0		10·61	·72	3·32	<·001>·0004*
breadth	9·1		7·80	·53	2·45	<·02>·012*
P_1 length		8·1	6·45	·50	3·30	<·001>·0004*
breadth		5·2	4·71	·35	1·42	>·05
length : breadth ratio ..		1·56	1·373	·119	1·57	>·05
P_2 length		12·4	10·05	·62	3·79	<·0004*
breadth		5·5	5·35	·25	·60	>·05
length : breadth ratio ..		2·25	1·879	·076	4·88	<·0004*
P_3 length		14·3	11·95	·54	4·37	<·0004*
breadth		6·3	6·08	·39	·56	>·05
length : breadth ratio ..		2·27	1·970	·130	2·30	<·03>·02
P_4 length		16·5	13·75	·79	3·48	<·0004*
breadth		7·3	7·11	·47	·40	>·05
length : breadth ratio ..		2·26	1·938	·100	3·22	<·003>·001*
M_1 breadth	E.C. 30 10·4		9·92	·52	·92	>·05

(ii) *Canis mesomelas* Schreber.

Specimens E.C.18-20, 22-27 and 29; various incomplete mandibular fragments.

Specimen E.C.31: isolated M_1.

Specimen E.C.32: isolated P_4.

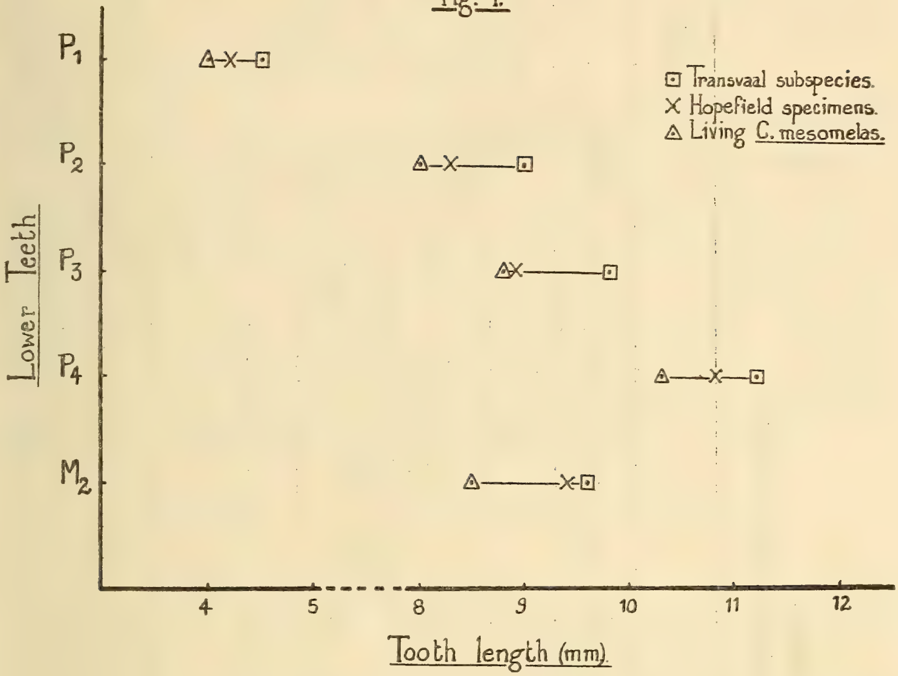
Specimen E.C.21: maxillary fragment bearing M^1 and M^2.

In another paper (Ewer, in the press) only a single character was found in which there was no overlap between the two living species of jackal, *Canis mesomelas* Schreber and *C. adustus* Sundevall, and which therefore allowed of a certain assignment of a single specimen to one or the other species. This character is the length of the carnassial tooth relative to that of the succeeding molar. This is referred to as the "carnassial: molar ratio" and either upper or lower ratios serve to separate the two species.

In the case of the material under discussion at present four specimens, E.C.18, 22, 25 and 26, include both M_1 and M_2 and therefore allow of the calculation of the lower carnassial: molar ratio. The values found are 2.03, 1.98, 2.10 and 2.30 respectively. For the samples of 14 *C. mesomelas* and 10 *C. adustus* used in the previous study the values range from 1.99 to 2.57 for the former and 1.60 to 1.81 for the latter. The Hopefield specimens clearly belong to *mesomelas*, and in the table of measurements the mean and range for the sample of extant *mesomelas* are given for comparison (table 5). It will be seen that although the means for the Hopefield specimens lie within the normal range for *mesomelas* a number of individual measurements lie beyond the upper size limit found for the living species.

A fossil subspecies of *C. mesomelas* has been described (Ewer, in the press) from the Transvaal deposits, differing from the living form principally in the fact that relative to the length of the carnassial M_2 is less reduced and the premolars are longer. It is therefore of some interest to compare the lengths of M_2 and of the premolars in the Hopefield specimens with the corresponding values for the Transvaal fossils. Figure 1 shows the mean values for the relevant dimensions, with those of the extant form for comparison. It will be seen that in each case the Hopefield value is intermediate between those for the Transvaal subspecies and for the living form. There seems to be little doubt that we are here dealing with a phylogenetic series in which a reduction of the molars and a shortening of the premolars is taking place; the Hopefield specimens representing a form ancestral to the living black-backed jackal and the Transvaal form in turn ancestral to the Hopefield. The functional significance of the changes is not at once apparent, and it may be that they would be better expressed by saying that a general reduction in overall size is taking place, but without any reduction in size of the carnassials, which therefore show an increase in relative size. Without

Fig. 1.



VALUES.

Length (mm.)	Transvaal	Hopefied.	Living.
P_1	4.5	4.2	4.0
P_2	9.0	8.3	8.0
P_3	9.8	8.9	8.8
P_4	11.2	10.8	10.3
M_2	9.6	9.4	8.5

whole skulls and skeletal material available it is not possible to decide whether this latter formulation is the more correct. It may be noted in passing that the Hopefield *Lycaon* also differs from the living species in possessing a longer premolar row.

A second fossil subspecies of *C. mesomelas* is known from African deposits. This is *Canis mesomelas latirostris* (Pohle) from Olduvai and Serengeti. This subspecies is distinguished from the living form by its very broad snout and shorter and less inflated auditory bulla. In the absence of a complete skull no adequate comparison of our material with this subspecies is possible, but Pohle (1928) gives measurements for the lengths of the teeth of his three specimens. The lower premolars resemble those of the Hopefield specimens in being rather longer than is usual in living *C. mesomelas*, but M_2 (present in

TABLE 5.

Measurements of teeth of fossil jackals compared with mean values for a sample of 14 living *Canis mesomelas*.

	Specimen No.														Living *C. mesomelas*	
	E.C. 18	E.C. 22	E.C. 26	E.C. 29	E.C. 25	E.C. 19	E.C. 31	E.C. 23	E.C. 32	E.C. 20	E.C. 24	E.C. 27	E.C. 21	Fossil Mean	Mean	Range
$P_{\bar{1}}$ length ..						4·2								4·2	4·0	4·8—3·4
breadth						2·8								2·8	2·7	3·2—2·3
$P_{\bar{2}}$ length ..						8·3								8·3	8·0	9·0—7·2
breadth						3·7								3·7	3·3	3·8—2·4
$P_{\bar{3}}$ length ..					8·9	9·1				9·7	7·9			8·9	8·8	10·0—7·1
breadth					3·7	3·9				3·9	3·2			3·7	3·5	4·0—3·0
$P_{\bar{4}}$ length ..				ca. 11·0	10·3	10·9			12·1	10·4	9·2	12·0		10·8	10·3	11·5—9·2
breadth					4·5	5·2			5·1	4·6	3·9	5·9		4·9	4·3	4·8—3·6
$M_{\bar{1}}$ length ..	20·3	19·0	21·1	ca. 17·9	17·6	19·2	17·9	18·2				ca. 90·0		18·7	18·8	20·7—16·5
breadth	8·7	7·7	8·6	ca. 7·7	6·8	8·8	7·1	7·5						7·9	7·2	8·2—6·5
$M_{\bar{2}}$ length ..	10·0	9·6	9·2	9·8	8·4									9·4	8·5	9·6—7·4
breadth	7·7	6·7	6·9	ca. 7·8	6·1									7·0	6·3	7·0—5·7
$M_{\bar{3}}$ length ..					3·6									3·6	4·2	4·9—3·5
breadth					3·4									3·4	3·8	4·3—3·3
$M^{\underline{1}}$ length ..													12·2	12·2	11·8	13·7—10·3
breadth													14·0	14·0	13·7	15·5—11·7
$M^{\underline{2}}$ length ..													7·9	7·9	6·8	7·8—6·2
breadth													10·5	10·5	10·5	11·5—9·8

2 specimens) is shorter than in the Hopefield material. In the absence of a skull it seems unwise to assign our material to Pohle's subspecies, particularly since the Transvaal subspecies does not show the characters of snout and bulla diagnostic for *C. mesomelas latirostris*.

The Hopefield specimens thus appear to be the middle term of a series leading from the Transvaal subspecies to the extant black-backed jackal. As must always be the case when a fossil record approaches completeness, this situation raises difficulties in nomenclature. The exact point as which a progressive change is taken to be of sufficient importance to warrant nomenclatural recognition must be largely a matter of individual judgment. In the present case it is felt that since the majority of measurements for the Hopefield specimens fall within the range of values found for the living specimens, the erection of a separate subspecies is not likely to be useful. Nevertheless, when questions of dating are being considered the intermediate character of the Hopefield specimens between the extant *C. mesomelas* and the Transvaal fossil subspecies must be borne in mind.

5. Family *Mustelidae*

Mellivora capensis (Schreber).

Specimen E.C.14: an almost perfect skull, with the zygomata missing (Pl. XXXII).

Specimen E.C.14 very closely resembles the living honey-badger, *Mellivora capensis* (Schreber), and differs only in its rather smaller size and the fact that the palate is considerably less prolonged posteriorly. The measurements of the fossil specimen are given below compared with those of the living form (table 6). It will be seen that although the fossil skull is considerably shorter than the mean for the sample of 15 living *Mellivora capensis* the variability of the latter is so high that the difference is not significant. The post-orbital width is significantly less in the fossil than in the living specimens; but when the smaller size of the fossil is taken into account, by expressing the post-orbital width as a percentage of the basilar length, the difference is no longer significant. The palate is, hower, significantly shorter in the fossil than in the living species, both absolutely and when expressed as a percentage of the basilar length.

The fossil specimen thus differs from extant *Mellivora capensis* only in having the palate less prolonged posteriorly. On the basis of a single specimen, and bearing in mind that the difference is significant only at the 2% level, it does not seem desirable to erect a separate subspecies for the Hopefield *Mellivora;* but, as has been emphasised before, the fact that the Hopefield specimen is distinguishable from the living species must not be lost sight of in considering problems of dating.

TABLE 6.

Measurements of Hopefield *Mellivora* compared with the corresponding measurements for a sample of 15 extant *M. capensis*. Symbols as before.

	Specimen E.C. 14	Extant *M. capensis* Mean	S.D.	$\frac{d}{\sigma}$	P
Basilar length	113·0	123·43	6·636	1·57	$>$·05
Palate length	50·4	60·65	4·389	2·34	$\simeq$·02*
Posterior palate width[1]	16·6	19·45	1·354	2·10	$<$·04$>$·03
Postorbital width	28·2	34·47	1·533	4·09	$<$·0004*
Maximum cranial width	63·0	65·81	3·540	·79	$>$·05
Width of nasal aperture	13·3	15·63	1·579	1·48	$>$·05
Length of P^4	10·8	12·67	1·133	1·65	$>$·05
Width of palate at level of P^4	39·6	45·33	3·114	1·84	$>$·05
Palate length as % of basilar length	44·60	49·226	1·990	2·32	$\simeq$·02*
Posterior palate width as % of basilar length	14·69	15·780	·968	1·13	$>$·05
Postorbital width as % of basilar length	24·96	28·026	1·704	1·80	$>$·05

[1] This is the width acros the posterior end of the hard plate.

III. Discussion.

The faunal remains described above may be considered in terms of the light they may throw on two problems: the date at which the Hopefield deposit was laid down, and the ecological nature of the locality at that time.

As regards the latter point the carnivore fauna adds little to our knowledge. All the species described are very similar to species which have existed within the area during historic times. One curious point is that although hyaenas and jackals are present, no remains of large carnivores, such as leopard and lion, have to date been discovered. Artiodactyl and horse remains are abundant, and it seems very improbable that in fact no large carnivore predators were present. It seems likely that further work may bring lion or leopard remains to light, and their absence cannot at this stage be taken as established.

As regards the date of the deposit it is quite clear on the one hand that it is much more recent than the Transvaal deposits. The species represented are all closely related to living forms, and no trace has been found of the archaic hyaenids, *Lycyaena* and *Leecyaena,* and the sabre-tooths which exist in the latter deposits. At the same time the fact that most of the specimens show slight differences from their living counterparts indicates that the deposit cannot be of very recent origin, but is likely to be at least as old as the upper Pleistocene. The Vlakkraal deposit in which was found the large *Lycaon* incisor previously mentioned is estimated to belong to the upper Pleistocene (Wells & Cooke 1942). Chemical analyses, carried out through the courtesy of Dr. K. Oakley of the British Museum, on a fragment of *Hyaena brunnea* mandible indicate that the fluorine content does not differ from that of the

human skull and of *Mesochoerus lategani*. The carnivore fossils *per se* do not provide any grounds on which it would be possible to decide whether the deposit belongs to the upper Pleistocene, as has been suggested (Singer & Keen, 1955), or is as old as the top of the middle Pleistocene.

SUMMARY

All the carnivore remains so far recovered from the Hopefield site are described. These include a new subspecies of *Lycaon*, *Lycaon pictus magnus*, a *Crocuta spelaea* and a jackal showing characters intermediate between the fossil subspecies from the Transvaal cave deposits and the living form, together with a *Hyaena brunnea* and a *Mellivora capensis*, each differing very slightly from the corresponding living form. In addition there are fragmentary remains of a viverrid resembling *Herpestes ichneumon* and a felid, probably *Leptailurus serval*.

It is concluded that the carnivore fauna is consistent with the upper Pleistocene dating which has previously been suggested for the deposit.

ACKNOWLEDGEMENTS

We are indebted to Dr. Hewitt of the Albany Museum, to Dr. K. H. Barnard of the South African Museum and to Mr. Skead of the Kaffrarian Museum for their allowing us every facility for studying skulls in their collections and for the loan of material. One of us (R.F.E.) is also indebted to the authorities of the British Museum (Natural History) for facilities for examining and measuring material in their collections, and to the South African Council for Scientific and Industrial Research for a research grant.

Mr. G. McManus, Department of Surgery, University of Cape Town, kindly photographed the specimens.

Part of a research grant from the Dr. C. L. Herman Research Fund of the University of Cape Town allocated to Drs. Singer and Keen was utilized for studying the carnivora.

One of us (R.S.) is indebted to the Wenner-Gren Foundation for Anthropological Research, New York, whose motor vehicle, donated to the University of Cape Town, is being extensively used for collection of material from the site.

Publication of this paper was assisted by a grant-in-aid made by the Council of the University of Cape Town.

REFERENCES

Broom, R. 1939. A preliminary account of the Pleistocene carnivores of the Transvaal caves. Ann. Transv. Mus. *19*, 331-338.

Drennan, M. R. 1954. Saldanha Man and his Associations. Amer. Anthropologist *56*, no. 5, 879-884.

Drennan, M. R. and Singer, R. 1955. A Mandibular Fragment, probably of the Saldanha Skull. Nature *175*, 364.

Ewer, R. F. 1954. The fossil carnivores of the Transvaal caves. The Hyaenidae of Kromdraai. Proc. Zool. Soc. Lond. *124*, 565-585.

Ewer, R. F. 1955. The fossil carnivores of the Transvaal caves. The Hyaenidae, other than *Lycyaena*, of Swartkrans and Sterkfontein. Ibid. *124*, 815-837.

Ewer, R. F. (in press). The fossil carnivores of the Transvaal caves. Canidae. *Ibid.*

Goldfuss, G. A. 1821. Osteologische Beiträge zur Kenntniss verschiedener Saügethiere der Vorwelt. Über die Höhlen-Hyäne (*Hyäne spelaea*). Nova. Acta Akad. Caes. Leop. 456-462.

Pohle, H. 1928. Die Raubtiere von Oldoway. Wiss. Ergeb. Oldoway-Expedit 1913. N.f. Hfr. 3. 45-54.

Roberts, A. 1951. The Mammals of South Africa. Published by the Trustees of the "Mammals of South Africa" Book Fund.

Singer, R. 1954. The Saldanha Skull from Hopefield, South Africa. Amer. J. Phys. Anthrop. n.s. 12, no. 3, 345-362.

Singer, R. and Keen, E. N. 1955. Fossil Suiformes from Hopefield. Ann. S. Afr. Mus. *42*, 169-179.

Wells, L. H. and Cooke, H. B. S. 1942. The associated fauna and culture of the Vlakkraal thermal springs, O.F.S. Trans. Roy. Soc. S. Afr. *29*, 203-233.

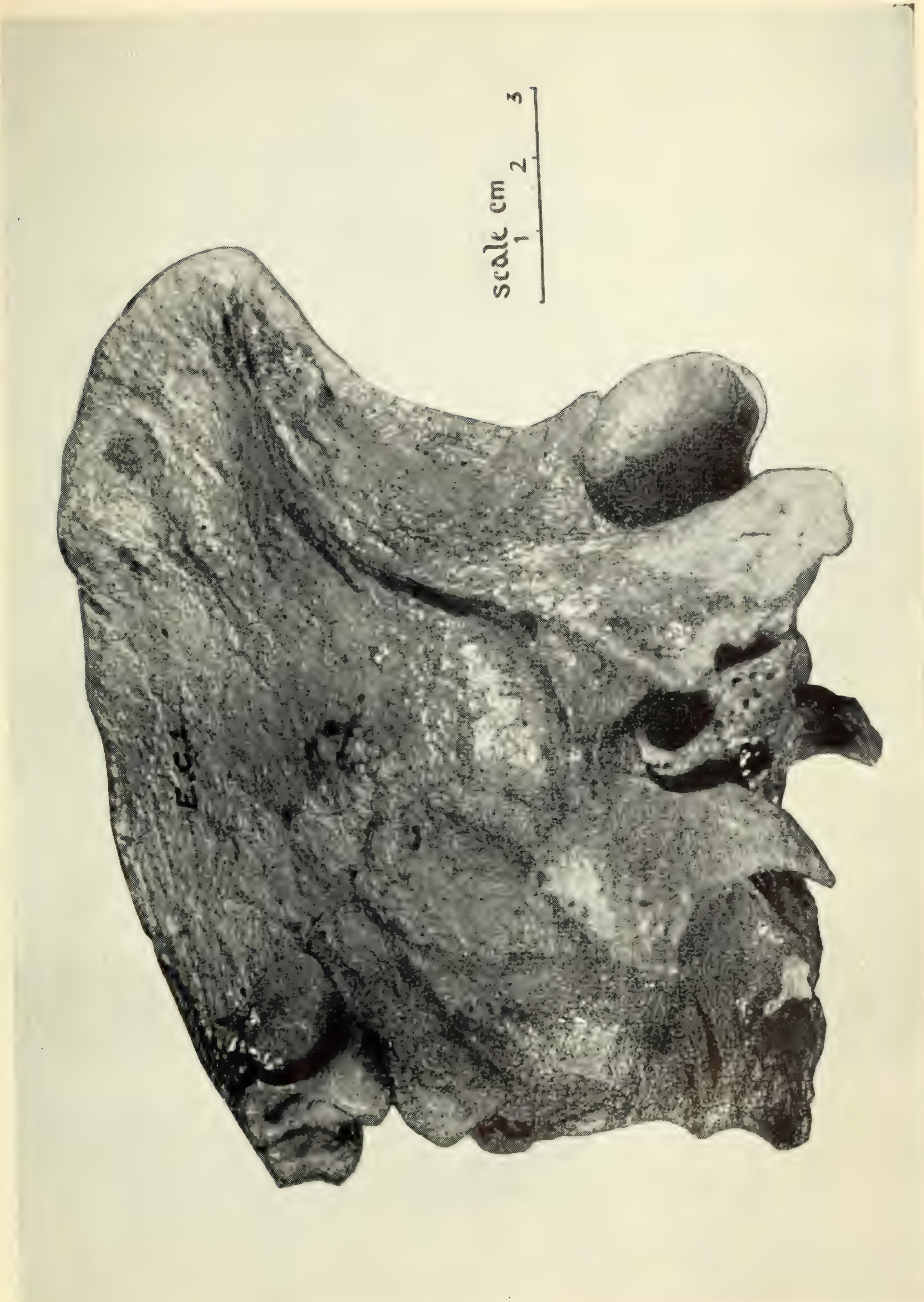


PLATE XXVII. *Crocuta spelaea* Goldf. Side view of specimen E.C.1.

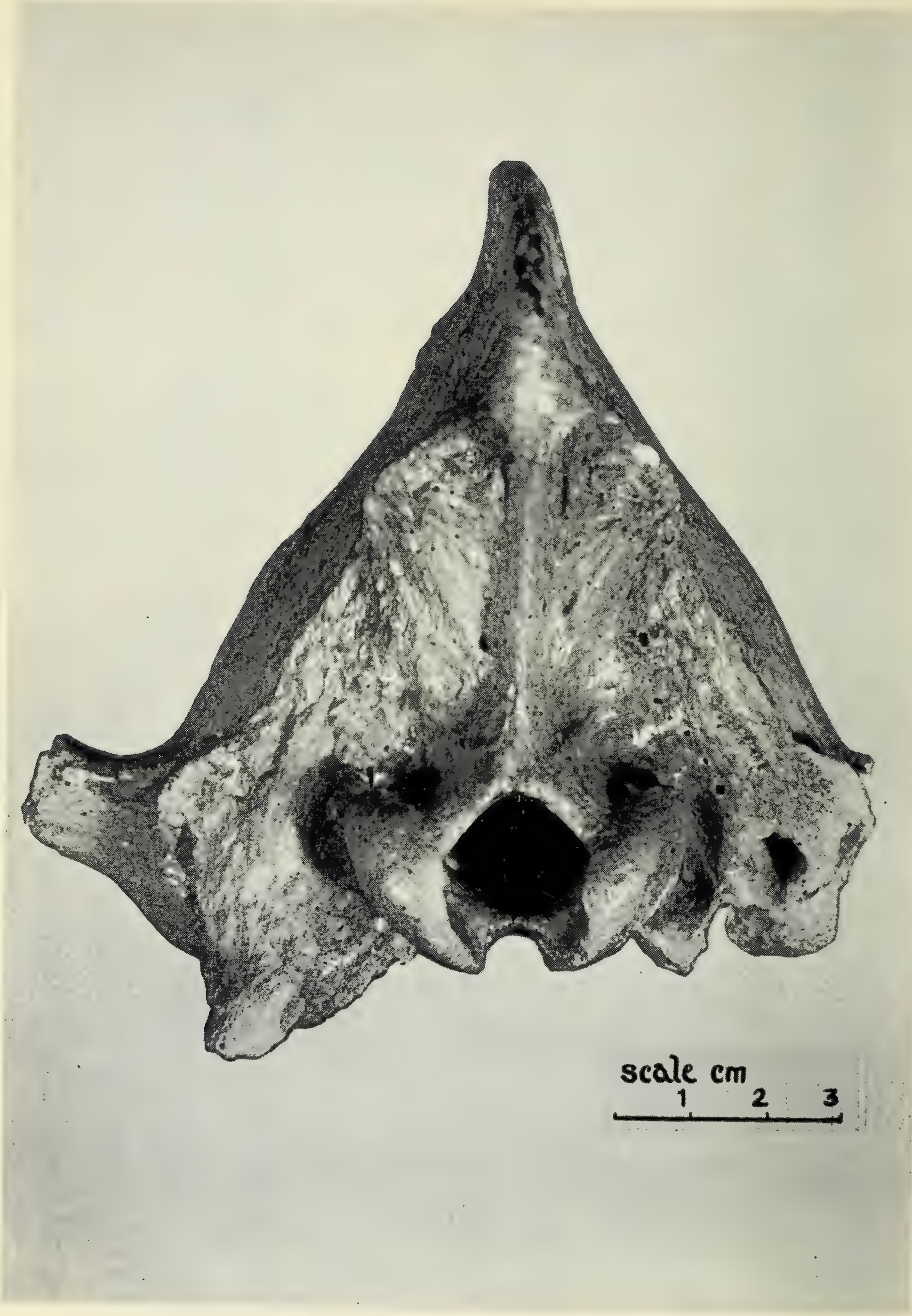


PLATE XXVIII. *Crocuta spelaea* Goldf. Posterior view of specimen E.C.1.

PLATE XXIX. *Crocuta spelaea* Goldf. Ventral view of specimen E.C.1.

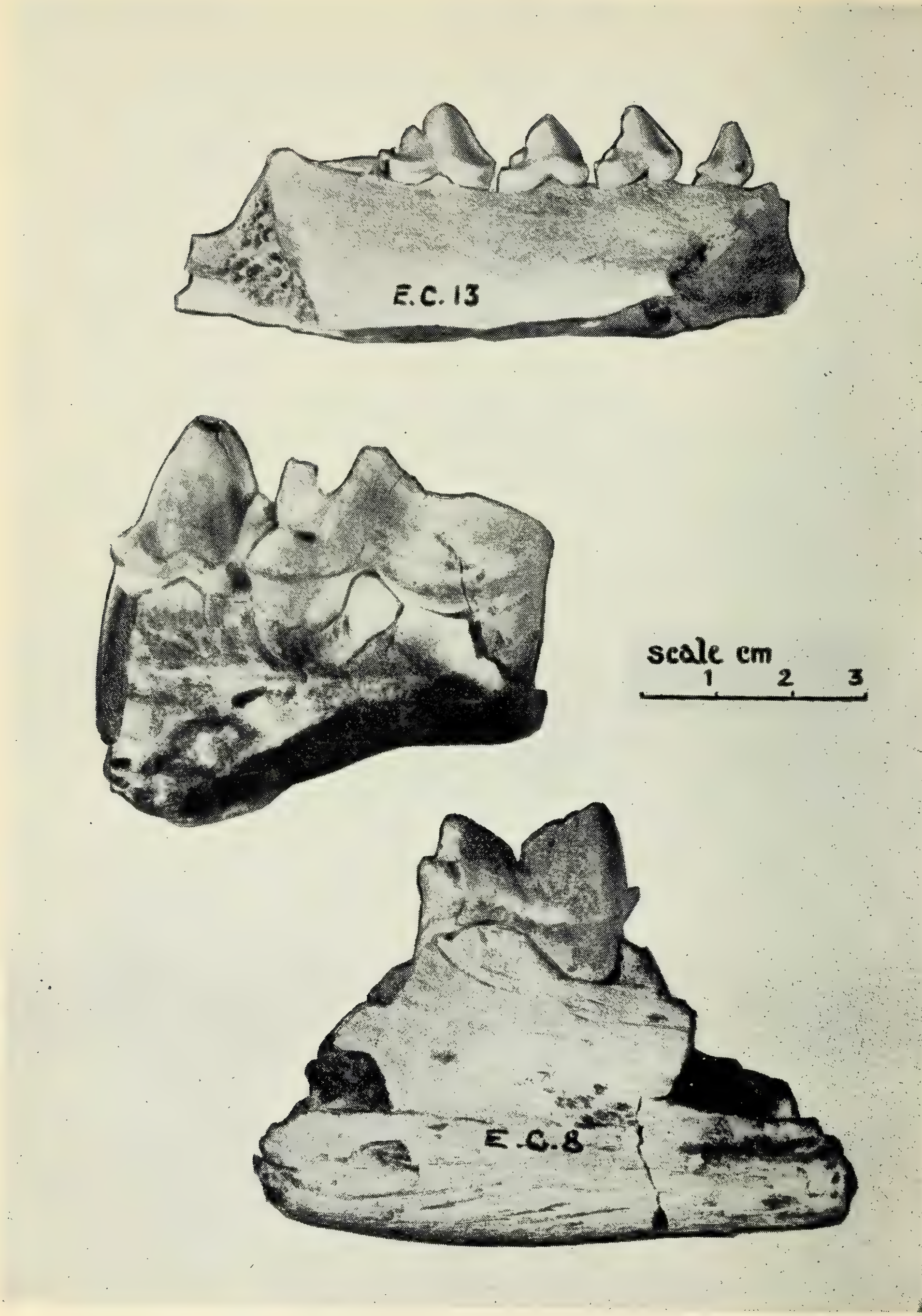


PLATE XXX. Lingual view of:
Top: *Lycaon pictus magnus* n.subsp. Specimen E.C.13.
Centre: *Crocuta spelaea*. Specimen E.C. 5.
Bottom: *Crocuta spelaea*. Specimen E.C.8.

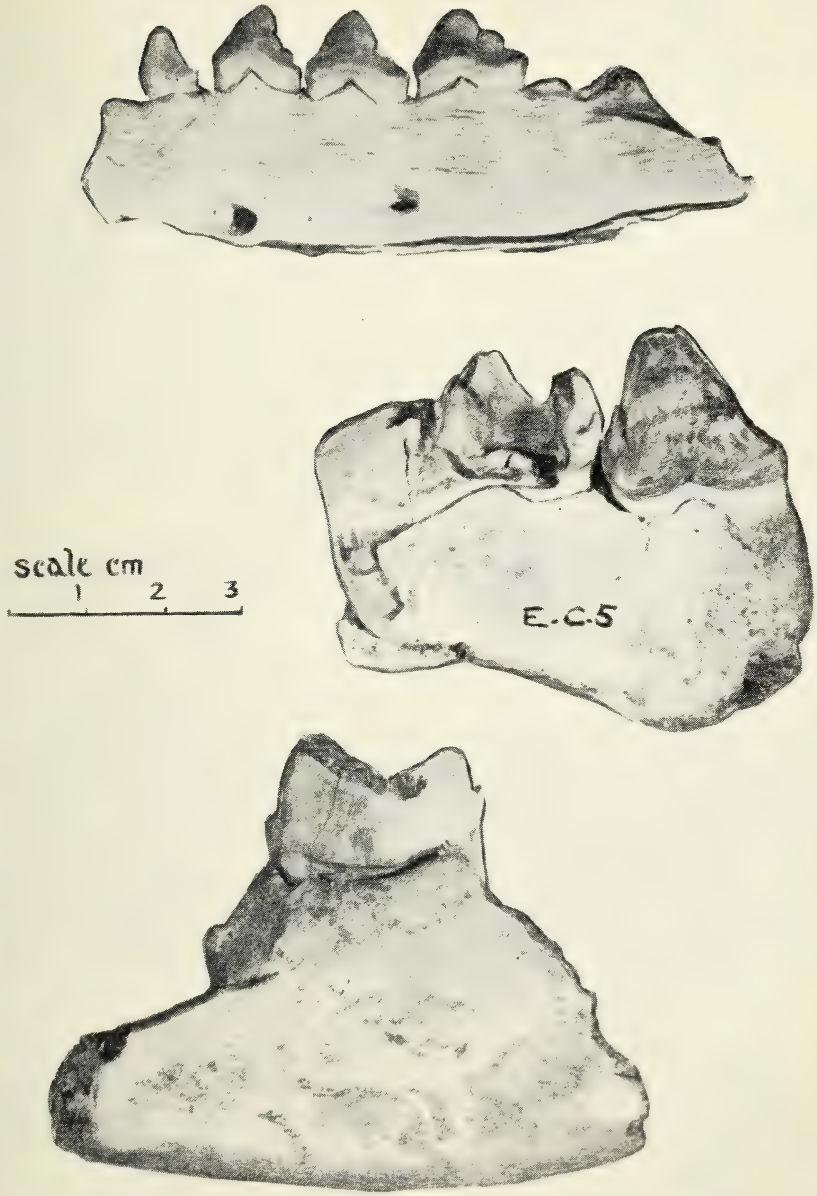


PLATE XXXI. Labial views of the specimens illustrated on Plate XXX.

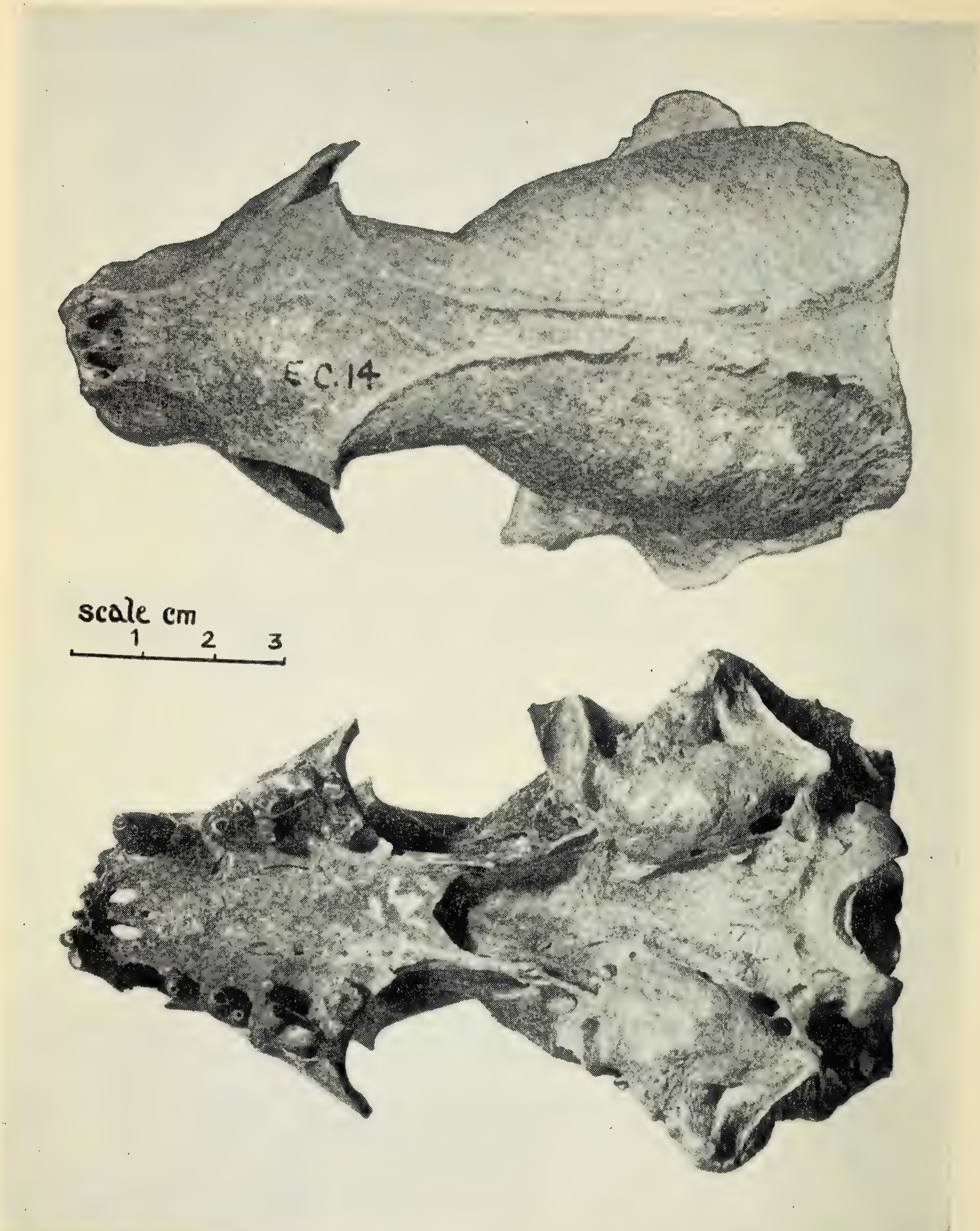


PLATE XXXII. *Mellivora capensis* (Schreber). Dorsal and palatal views of specimen E.C.14.

18. *Further Fossil Suidae from Hopefield*. By E. N. KEEN and R. SINGER, Anatomy Department, University of Cape Town.

(With Plates XXXIII-XXXV.)

INTRODUCTION

In a previous publication (Singer and Keen, 1955) the available suid material from the fossil site on the farm "Elandsfontein" was ascribed to a single new species *Mesochoerus lategani*. Subsequently, on a number of field trips, one of us (R.S.) and a medical student, A. J. van Niekerk, recovered not only further specimens of the above genus, but also a fragment of a mandible containing deciduous third and fourth molars and a permanent unworn first molar (specimen S. 22) of this genus, as well as a second and third molar (probably upper) of a different genus, namely *Tapinochoerus*.

It is the purpose of this paper to describe the new material in the Anatomy Department:—

A. The additional *Mesochoerus* specimens so as to increase the range of variation in *Mesochoerus lategani* and to evaluate the status of this species better, and to describe a specimen (S.28) of *Mesochoerus paiceae*.

B. The milk dentition in the fragment of mandible numbered S.22.

C. The *Tapinochoerus* specimen (S.26) and to establish its specific rank.

DESCRIPTION AND DISCUSSION

A. Genus MESOCHOERUS Shaw and Cooke

DESCRIPTION

1. *Mesochoerus lategani* Singer and Keen.

The general description of these four specimens (S.23, 24, 25, 27) is the same as in our previously published material (1955), and it is only necessary to note the specimens and their dimensions, and to outline any additional distinctive features.

Specimen S.23: A left upper third molar in which the posterior part of the talon consists of only one pillar behind the third lateral pair. This single pillar is vertically grooved as if in partial separation. The anterior median pillar and its outriders project beyond the root margin giving the tooth a pronounced rounded bulge anteriorly, well seen in side view (Pl. XXXIII A). On reviewing our specimens, this feature is seen in all the third molars particularly when in early wear. It is also observed in *Metridiochoerus* as well as in *Mesochoerus olduvaiensis* and *paiceae*, while in *Sus limnetes* from Omo (now classified as *Koiropotamus* = *Potamochoerus* by Hopwood and Hollyfield, 1954) the anterior median pillar and its outriders form a separate plate. In *Notochoerus* and *Phacochoerus* species the bulge is absent.

Specimen S.24: A left upper third molar in which the talon behind the third lateral pair consists of 5 small pillars. The buccal pillar of the second lateral pair also has an accessory nodule anterior to and confluent with it. Specimens S.23 and S.24 are in approximately the same stage of late wear, yet in S.23 the posterior pillars are fused into one massive posterior median pillar. This variation in number of pillars in the talon has already been commented on in our previous publication.

Specimen S.25: A right upper third molar whose front portion is missing as it is broken through the anterior pair of lateral pillars. The lingual surface of the 2nd and 3rd lateral pillars shows two deep vertical grooves, giving an exaggerated appearance not yet encountered in this species and suggestive of incomplete fusion of the cones which form the complex occlusal pattern of the teeth (Pl. XXXIII B). Viewed from the occlusal aspect the tooth presents an unusual concave curvature on the labial side of the posterior part of the tooth (Pl. XXXIII C) which is produced by a bulge at the crown-root junction of the 2nd lateral pillar. The roots are missing.

Specimen S.27: An almost complete right upper third molar. The anterior pair of roots are broken off, and a small piece of the central portion of the first lateral pillar on the lingual side is missing. The part of the talon behind the 3rd lateral pair in this massive tooth also consists of 5 pillars. The anterior median pillar and its outriders are so large as to almost form a separate plate, while the 2nd lateral pillar on the lingual side has an accessory cone in front of it (compare S.24) while the pillar on the buccal side has a small nodule projecting up in front of it at the cingulum. The buccal pillar of the 3rd lateral pair has 3 small accessory nodules on its outer side. The outer root of the 2nd pair of lateral pillars, though broken near its tip, is projecting back acutely to overlap and cover the plate-like roots of the 3rd pillar with which it is partially fused just below the crown-root junction (Pl. XXXIII D).

Specimen.	Maximum Length.	Maximum Breadth.	Occlusal Breadth.	Height of unworn pillars above root.
S.23	60.0	25.4	21.2	—
S.24	59.0	25.9	21.4	26.0 (posterior)
S.25	—	c.27	c.25	30.0 (posterior)
S.27	69.5	29.7	24.2	28.0 (posterior)
Range of previous specimens (7)	63-70	24-28	20-23	22-35

TABLE I: *Dimensions of the crowns of the upper third molars* (mm.).

The length of S.23 and S.24 might appear to exclude them from the range of variation revealed by the previous series. However, in the previously described series of lower third molars, of which 6 could be measured, the smallest was 67 mm. long, while the other 5 ranged from 73 to 77 mm. (mean 75 mm.), but there seemed to be no other reasons for excluding the short tooth from the series. In the same way, the shortness of S.23 and S. 24 will not exclude these two upper molars, identical in all other respects, from the species. The range of variation in length is now increased to 59-70 mm. Bearing in mind the following description of a different species of *Mesochoerus* from our site, and also that no upper teeth of *Mesochoerus paiceae* have previously been described for comparison, there is a possibility that the smaller upper teeth which we have included in our range for *Mesochoerus lategani* (e.g., S.24) may yet prove to be the uppers of *Mesochoerus paiceae.*

From table 1 it is also seen that S.25 and S. 27 are at the upper end of the range of variation for maximum breadth, and actually S.27 outstrips the other specimens and increases the upper end of the range to 29.7 mm.

2. *Mesochoerus paiceae* Broom.

Specimen S.28: A mandibular fragment containing a right third molar tooth in early wear. There are only 4 pairs of lateral pillars and these are more widely separted from each other than in *Mesochoerus lategani* specimens. The pillars taper to a pointed occlusal end, their bases being wide and partially fused at the cingulum. The 2nd lateral pillar on the labial side has an accessory cone anterior to it (Pl. XXXIII E). The anterior median pillar is pushed somewhat to the lingual side by a large outrider which is continuous with 6 low nodules fused together to form a plate anterior to the anterior median pillar.

Dimensions of S.28 (mm.):—

Maximum length	65.0
Maximum breadth	24.1
Occlusal breadth	17.7
Height of unworn 3rd pillar above root	31.5

The individual dimensions of this tooth fall within the previously reported range of *Mesochoerus lategani*, with the exception of the maximum length which is 2 mm. short of the lower end of the range. In itself this would have been of minor importance. Hower, there are only 4 pairs of well-separated lateral pillars, as compared with 5 pairs in *lategani*, and behind the fourth pair is a single undivided median pillar. In addition, despite its shortness, the breadth is at the upper limit of our previous range. Taking these 3 points into consideration, it cannot be distinguished from the 2 specimens (Broom's type and Shaw and Cooke's neotype) on which *Mesochoerus paiceae* is based.

Discussion

Since our previous publication on the Hopefield *Suidae*, Hopwood and Hollyfield's monograph (1954) has been received. In this they classify *Mesochoerus* with *Hylochoerus*, hereby following Arambourg (1947), although the latter was not quite certain of this attribution. We have weighed up this opinion in the light of the reasons which led Shaw and Cooke (1941) to decide that their genus should be separated from *Hylochoerus*. Briefly, these were that the third molars were elongated and not so brachyodont as in *Hylochoerus*, and that the premolars were not reduced as in the modern animal. These points remain, in our opinion, ample justification for maintaining the genus *Mesochoerus* which now comprises three species, namely, *paiceae*, *olduvaiensis* and *lategani*. Leakey's *Mesochoerus heseloni* has been attributed by Arambourg (1947) to *Omochoerus*. However, Leakey (personal communication, 1955) still maintains that *Omochoerus* should be included under *Mesochoerus*. Consequently the position of *heseloni* is held in abeyance. On a phylogenetic sequence, *Mesochoerus* would seem a logical intermediate stage between *Hylochoerus* and *Metridiochoerus*. This problem may finally be resolved by further discoveries, particularly of tusks and other skeletal remains.

The specimen S.28, as described above, cannot be grouped with the previously described M_3 specimens of *Mesochoerus lategani*. Its dimensions and general appearance are such that it must be identified as *Mesochoerus paiceae*. In our previous series S.21 was included on the assumption that a 5th pair of lateral pillars was broken away posteriorly. Re-examination of this specimen, in the light of the fresh discovery, makes this seem less likely, and S.21 may represent a second example of a tooth which must be referred to the genotype *paiceae*.

B. MESOCHOERUS Milk Dentition

Specimen S.22: A left mandibular fragment bearing an unworn M_1, D_4 and a root fragment of D_3 (Pl. XXXIV).

Dimensions of the fragment:—

Total length	77 mm.
Maximum breadth	24 mm.
Height of mandible at M_1	29 mm.

The *first molar* is unworn and is composed of 2 pairs of lateral pillars with a double median pillar between and separating them, small anterior outriders, and a large complex posterior median pillar. The posterior lobe of the tooth is broader than the anterior, and its 2 pillars are more separated from each other. The enamel is coarsely rugose and its irregularities form a pattern which is best seen on the labial side of the posterior lobe. The anterior and posterior lateral pillars fuse with each other about 4 mm. above the cingulum, and the posterior median pillar fuses with the posterior lateral pillar on both sides. The cingulum is only slightly developed. There are 4 roots which cannot be directly inspected as they are embedded in the mandible, but they were examined on a skiagram. The posterior roots are larger than the anterior.

Dimensions of M_1 (mm.):—

Maximum length	23
Maximum breadth (posteriorly)	13
Height of crown (anteriorly)	16
Height of crown (posteriorly)	15
Root length	*c.*15

Behind the tooth is a broad incomplete cavity which presumably contained the developing M_2. The breadth of the mandible diminishes noticeably behind M_1, and there are no signs of root canals from the cavity for M_2.

The *last (fourth) deciduous molar* is a trilobed tooth with 3 roots on the labial side and 2 on the lingual side. It is in moderate wear. The 3 pairs of lateral pillars increase in size and decrease in wear from front to back. The 2nd lingual pillar is broken. The general appearance of the tooth is seen in Plate XXXIV. Examination of the fragment and of the skiagram reveals that the roots of this tooth straddle a cavity which one would have expected to contain the developing tooth germ of P_4. This cavity communicates widely with the mandibular canal and it seems logical to assume escape of the tooth germ through this opening. A skiagram of the mandible of a modern domestic pig at about the same stage of development shows an unerupted tooth resting in a cavity at exactly the same position in relation to D_4 as in the fossil specimen.

Dimensions of D_4 (mm.):—

Maximum length	24
Maximum breadth at cingulum (posteriorly)	11
Maximum length of roots (from X-ray)	c.18

The *third deciduous molar* is only represented by a root fragment resting in one of the 2 alveolar root canals in front of D_4.

The bulk of the suid remains collected from Elandsfontein have proved to belong to the genus *Mesochoerus*. The dimensions of M_1 of S.22 compare very favourably with those of the 2 worn M_1 teeth of *Mesochoerus lategani* previously described, especially if the measurements are taken close to the cingulum. The unworn height of the crown (16 mm.) compares reasonably with the unworn height of M_3 (3rd pillar), which averaged 29 mm. in 4 specimens in which it could be accurately measured. The ratio of the unworn height of M_1/M_3 is thus 1 : 1.8. There seems good reason to conclude that this specimen is derived from a young *Mesochoerus*.

C. Genus Tapinochoerus van Hoepen and van Hoepen

Tapinochoerus meadowsi Broom

Description

Specimen S.26: A third and a second molar, found lying in apposition, were subsequently joined together with plaster-of-paris. The second molar is partially embedded in bone. The third molar resembles the tooth on which Broom (1928) originally based the species *Notochoerus meadowsi* (= *Tapinochoerus meadowsi*, Cooke, 1949). One of us (R.S.) examined specimens of *Tapinochoerus meadowsi* from the Transvaal Museum (S.K.? 387, S.K.? 388, B.F.1) now being studied by Dr. R. F. Ewer, Rhodes University, Grahamstown. The former two specimens are lower M_3 probably from the same jaw, and B.F.1 is a part of a skull, briefly described by Broom, 1948, containing unerupted M^3 teeth and partially worn M^2 teeth. As a result of careful comparison, S.26 is considered to consist of left upper molars.

Left upper third molar: The general structure of the tooth is phacochoeroid consisting of two rows of lateral pillars separated by intermediate pillars. The anterior pair of lateral pillars is in full wear and constitutes the first lobe. The pair behind this is just coming into wear (Pl. XXXV). Posterior to this the unerupted portion of the tooth falls away sharply at an angle of about 45°. This part of the tooth consists of a large number of pillars (probably constituting 3 lobes) on each side with an intermediate pillar between

each pair. These lobes are less separated than the type specimen, but exhibit a similar appearance to S.K.? 387. The extreme posterior end of the tooth is broken off. The anterior lobe is broader than the second, and is rounded anteriorly in the occlusal view, with a slight constriction separating it from the 2nd lobe. The anterior extremity of the lobe consists of a number of circular and irregularly shaped nodules which cause an anterior bulging obvious in the lateral view (Pl. XXXV). The worn surface of the lateral pillars of this lobe are H-shaped with the inner pair of lobules equal in size and parallel to the outer pair. The bases of all the pillars are flattened from side to side, and are open; no roots are apparent. This is a typical phacochoeroid appearance. The cement covering the tooth is scanty.

Three third molar teeth from the Olduvai Gorge (Coryndon Museum, Old. B.K.II, Ex. 1953, nos. 109, 160, 448), studied by R. S., are almost identical in general appearance, with the posterior unworn part of the tooth falling away sharply at an angle of about 45° from the anterior plane of wear. The degree of separation of the pillars varies in the 3 specimens, being more marked in 109 and 448, but the same as S.26 in 160. However, in the latter the outer enamel is thicker and the tooth as a whole is broader.

Specimen.	Maximum Length.	Maximum Breadth.	Occlusal Breadth.	Height of worn anterior pillar.	Maximum Height.
S.26	c.74	21.5	19.2	63.8	70.0 (2nd lobe)
Type specimen	76	19	16	55	64
S.K.?387	—	19.1	15.7	53.1	68.3 (3rd lobe)
S.K.?388	—	19.1	15.9	53.0	c.67 (3rd lobe)
Old.B.K.II.109	—	19.5	16.8	—	—
Old.B.K.II.160	c.71	20.8	19.1	78.0	99.6 (3rd lobe)
Old.B.K.II.448	—	17.4	17.0	—	—

TABLE II: Dimensions of S.26 compared with those of other third molars (mm.). The height of 109 and 448 could not be determined precisely, but the maximum height was considerably in excess of 70 mm. The lengths of S.K.? 387 and 388 and Old. 109 were more than 65 mm. The Swartkrans specimens are not fully erupted; therefore less than full-grown length.

Left upper second molar: This closely resembles the M^2 of B.F.1 which has not yet been described in detail (Broom, 1948). Our specimen is phacochoeroid in appearance and consists of 2 lobes which are less separated from each other than in B.F.1. Each lobe has a separate pair of roots. The anterior roots are smaller than the posterior ones, and the lingual pair smaller than the labial pair. There is a fairly well-marked cingulum anteriorly and the posterior aspect of the posterior lobe bulges back to meet the forward projection of the third molar. The bulge posteriorly of the heel is even more accentuated in B.F.1. The crown of the tooth is worn in the same plane as the anterior lobe of M^3 (Pl. XXXV).

The occlusal pattern of the anterior lobe appears to consist of 2 lateral pillars fused with an anterior median pillar, and the advanced stage of wear has left 3 enamel islands within an enamel outline forming two-thirds of a circle anteriorly and an irregular border posteriorly. The posterior lobe appears to consist of 2 lateral pillars which have fused in a most irregular manner with an anterior median, a middle and 2 posterior pillars (Pl. XXXV).

Specimen.	Maximum Length.	Maximum Breadth.	Occlusal Breadth.	Height above cingulum.
S.26	31.8	19.0	18.2	19.1 (anterior lobe) 22.3 (posterior lobe)
B.F.1	35.2	18.6	17.5	—

TABLE III: Dimensions of M^2 (mm.). In S.26 the maximum length is the same as the occlusal length. Height not measured in B.F.1 because junction between crown and root not clear.

There is no doubt that S.26 must be identified with the species originally named *Notochoerus meadowsi* by Broom (1928).

Discussion

In efforts to reduce the number of genera of African fossil *Suidae*, Hopwood and Hollyfield (1945) and Arambourg (1947) found Broom's species difficult to place. Arambourg (1947) discussed the evolution of the phacochoeres in some detail and erected a phylogenetic series based on increasing height of the teeth, increasing length of the third molars, and decreasing separation of the constituent columns of the third molars. Assuming an origin in some ancestor resembling *Sus* or *Potamochoerus*, his series runs through *Hylochoerus* to *Metridiochoerus* Hopwood, and then *Notochoerus* Broom as a logical step to *Phacochoerus*. Without discussing the height or the poor separation of the columns of the tooth on which it was based, Arambourg agreed with Broom's original attribution of the species to *Notochoerus*. Hopwood and Hollyfield (1954), evidently unhappy with this opinion, included the species in *Metridiochoerus* Hopwood 1926. The height and length of the specimen, compared with those of the genotype *Metridiochoerus andrewsi*, make them uneasy companions.

A similar difference of opinion, in the opposite direction, shows that these authorities are not wholly in agreement over the definition of the two genera. Arambourg (1947) considered that *Notochoerus dietrichi* Hopwood 1934 should be included in *Metridiochoerus*; Hopwood and Hollyfield persist in the opinion that this is a *Notochoerus*.

The mean dimensions and characters of the upper and lower third molars in previously described *Metridiochoerus andrewsi* specimens may be summarised as follows: maximum length *c*.60 mm., length of talon (i.e. portion

behind the first 2 lobes) *c* 25 mm., maximum breadth 20-28 mm., unworn height of crown 50 mm. or less; roots fairly well developed. *Notochoerus capensis* third molars have the following characteristics: the tooth is greatly elongated (max. length 80-100 mm.) by development of the talon (length 50-70 mm.), maximum breadth is 22-30 mm., and unworn height is *c* 50-60 mm.; roots are well developed and lateral columns are fairly well separated from each other. The original *Notochoerus meadowsi* and those third molars which have been classified with it under the generic name *Tapinochoerus* may similarly be summarised: maximum length 70-75 mm., length of talon 35-40 mm., maximum breadth 15-20 mm., unworn height of crown 65-80 mm. Here the columns are closely packed and there is very little root formation, the tooth as a whole having a marked phacochoeroid appearance. The dimensions of the specimens noted and described in this paper increase these ranges. The degree of separation of the columns (pillars) in these specimens varies, but none exhibit the fairly marked separation of *Notochoerus capensis*.

These measurements, together with the general appearance of the teeth in question, make it in our view unjustifiable to classify *meadowsi* specimens as either *Notochoerus* (after Arambourg, 1947) or as *Metridiochoerus* (after Hopwood and Hollyfield, 1954). In the phylogenetic sequence *Metridiochoerus-Notochoerus-Phacochoerus*, the *meadowsi* specimens form a natural link between *Notochoerus* and *Phacochoerus*. We therefore prefer to retain the genus *Tapinochoerus*. with two species, *meadowsi* Broom 1928 and *modestus* van Hoepen and van Hoepen, 1932. The latter, which is the genotype, is based on a considerably smaller third molar recovered from Cornelia, Orange Free State.

It might be argued that *Tapinochoerus* in this sense does not deserve separation from *Phacochoerus*. Cooke (1949) wrote: "Very possibly this may be regarded as only a sub-genus of *Phacochoerus*." Arambourg (1947) stressed the existence in early Quarternary times of a primitive form of *Phacochoerus africanus*, larger than the modern types and showing slightly greater complexity of enamel pattern. To this he gave the subspecific name, first used by van Hoepen and van Hoepen (1932), of *Phacochoerus africanus fossilis*. Whether this concept should be broadened to include the teeth under discussion is, in our opinion, doubtful. We prefer to regard the differences between these teeth and *Phacochoerus* as of generic rank.

Conclusion

The presence of a second genus *Tapinochoerus*, which at Olduvai is found in Beds II and IV and at Olorgesailie in deposits contemporary with the upper part of Bed IV, as well as two *Mesochoerus* species, one of which is similar to *olduvaiensis* found in Beds II and IV, tends to refute the previous

hypothesis of the persistence of an isolated species at "Elandsfontein" (Singer and Keen, 1955). Because *Tapinochoerus* and *Mesochoerus* have been recovered from various parts of South Africa (Vaal River, Swartkrans, Cornelia) as well as from East and Central Africa, it would now appear unnecessary to postulate isolation and subsequent evolution of a new species in the Cape. "Elandsfontein" at Hopefield therefore reflects the widespread distribution of at least these two suid genera.

The large number of species and genera on record at present may indicate that if a sufficient number of specimens were recovered the true intraspecific and intrageneric ranges of variation would appear, and would allow considerable merging of the closely overlapping types, so diminishing the number of genera and species recognized. On the other hand, it may reflect rapid evolutionary development in several directions produced by habitat and other selective factors.

The discovery of *Tapinochoerus*, which at Olduvai is relatively archaic, and, in the Vaal River sites is found in the younger gravels, strengthens the conclusion previously suggested (Singer and Keen, 1955; Singer, 1955) that the Hopefield deposits should be assigned conservatively to the early Upper Pleistocene period, equivalent to the interpluvial between the Kanjeran pluvial and the first Gamblian pluvial of East African chronology, a period now recognized as being the final phase of the Kanjeran pluvial.

SUMMARY

1. Four additional upper third molars of *Mesochoerus lategani* are described, thus increasing the range of variation of the species and improving the previously described diagnostic characteristics. Another specimen, identical to *Mesochoerus paiceae*, is described, and, a specimen previously included with *Mesochoerus lategani* is now referred to *paiceae*. There is also a short discussion on maintaining the rank of *Mesochoerus*.

2. The fourth deciduous molar and a first molar in a young *Mesochoerus* mandible are described.

3. Fossil M^3 and M^2 are identified with the species originally described as *Notochoerus meadowsi* by Broom (1928). Reasons are given for disagreeing with opinion expressed that this species belongs to *Metridiochoerus* or *Notochoerus* and for maintaining the use of the name *Tapinochoerus* to indicate a genus intermediate between *Notochoerus* and *Phacochoerus*.

4. The presence of *Tapinochoerus meadowsi* and 2 species of *Mesochoerus*, considered in conjunction with the other extinct and extant forms found on the farm "Elandsfontein" at Hopefield, strengtherns our view that the deposit may be referred conservatively to an early Upper Pleistocene period.

ACKNOWLEDGEMENTS

Mr. G. McManus of the Surgery Department kindly photographed the specimens.

Part of a grant to us from the Dr. C. L. Herman Research Fund of the University of Cape Town was utilized for field trips and technical assistance.

The Land Rover donated by the Wenner-Gren Foundation for Anthropological Research, New York, was used for the field trips.

One of us (R.S.) is indebted to the following for their permission to study their material and to include in this paper observations and measurements made thereon:

Dr. L. S. B. Leakey, Curator, Coryndon Museum, Nairobi;

Dr. A. C. Hoffman, Director, Nasionale Museum, Bloemfontein;

Dr. R. F. Ewer, Zoology Dept., Rhodes University, Grahamstown; and Dr. J. T. Robinson, Dept. of Vertebrate Palaeontology, Transvaal Museum.

Grants from the Council for Scientific and Industrial Research, the Wenner-Gren Foundation and the Dr. C. L. Herman Research Fund made possible visits by R.S. to these institutions for studying suid and other material.

Dr. K. H. Barnard, Director of the South African Museum, Cape Town has at all times given us access to extant comparative material, and we are also grateful to him for his advice and co-operation in the publication of this paper.

REFERENCES

Arambourg, C. 1947. Mission Scientifique de L'Omo, Tome I, Fascicule III; Paléontologie.

Broom, R. 1928. On some New Mammals from the Diamond Gravels of the Kimberley District, Ann. S. Afr. Mus., *22*, 439-444.

Broom, R. 1948. Some South African Pliocene and Pleistocene Mammals, Ann. Transv. Mus., *21*, 1-38.

Cooke, H. B. S. 1949. The Fossil Suina of South Africa, Trans. Roy. Soc., S. Africa, *32*, 1-44.

Hopwood, A. T. and Hollyfield, J. P. 1954. Fossil Mammals of Africa No. 8. An Annotated Bibliography of the Fossil Mammals of Africa (1742-1950). London British Museum (Natural History).

Middleton-Shaw, J. C. and Cooke, H. B. S. 1941. New Fossil Pig remains from the Vaal River Gravels, Trans. Roy. Soc., S. Africa, *28*, 293-299.

Singer, R. 1955. Investigations at Hopefield. Paper presented at Third Pan-African Congress on Prehistory, Livingstone. Published in summary in Congress Programme, and to be published in the "Proceedings".

Singer, R. and Keen, E. N. 1955. Fossil Suiformes from Hopefield. Ann. S. Afr. Mus., *42*, part 3, 169-179.

Van Hoepen, E. C. N. and Van Hoepen, H. E. 1932. Vrystaatse Wilde Varke, Pal. Nav. Nas. Mus. Bloemfontein, *2*, 39-62.

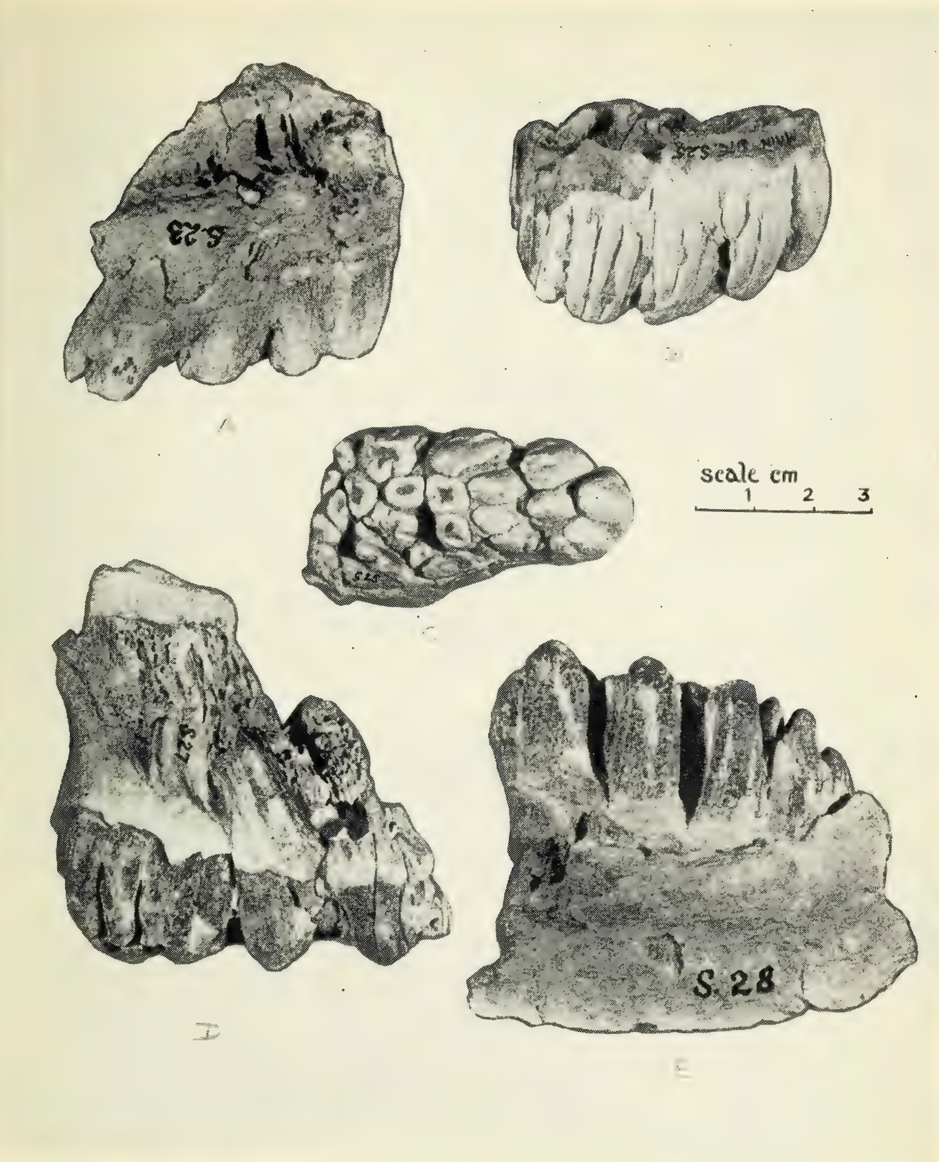


PLATE XXXIII. *Mesochoerus lategani* Singer & Keen.

A. Buccal (lateral) view of left upper molar (S 23).
B. C. Lingual (medial) and occlusal views of right upper third molar (S 25).
D. Buccal view of right upper third molar (S 27).

Mesochoerus paiceae Broom.

E. Lingual view of right lower third molar (S 28).

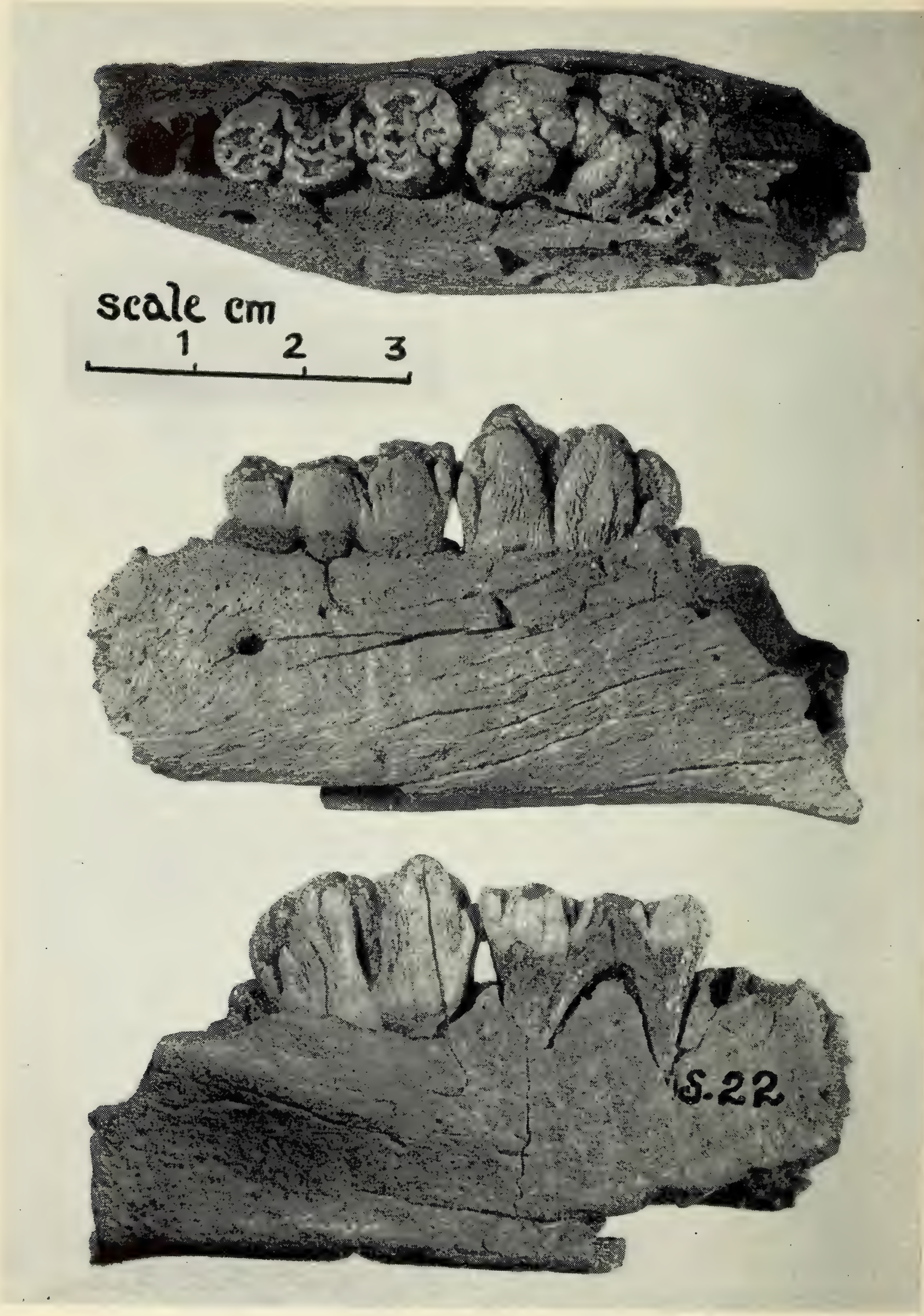


PLATE XXXIV. Occlusal, buccal (lateral) and lingual (medial) views of mandibular fragment of young *Mesochoerus* (S 22).

PLATE XXXV. *Tapinochoerus meadowsi* (Broom). Occlusal, lingual (medial) and buccal (lateral) views of left upper second and third molars.